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# The Cenozoic Brachiopod *Terebratula*: its type species, neotype, and other included species

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**SYNOPSIS.** *Terebratula terebratula* (Linnaeus, 1758) has a long and complex history. The specimen now recognised as the type was first illustrated by Colonna in 1616, and the first use of '*Terebratula*' is attributed to Lhwyd, 1699. Colonna's specimen was refigured by Klein, 1753, and the species *Anomia terebratula* was described by Linnaeus, 1758, with reference to the Colonna and Klein illustrations. The genus *Terebratula* was proposed by Müller in 1776, and *Anomia terebratula* Linnaeus designated as the type species by Lamarck in 1799, although it was not an originally included species. In spite of this history, the type of the genus was never formally ratified, the whereabouts of the type specimen was unknown, and the age and exact position of the type locality was uncertain. This paper summarises the history of *Terebratula terebratula* (Linnaeus) from 1616. *Anomia terebratula* Linnaeus is now accepted as the type species of *Terebratula* (ICZN ruling, 2000). We have collected new material from a locality near Andria, Italy, from which Colonna collected specimens of *Terebratula*, and selected a neotype from the Calcarenite di Gravina Formation which is Pliocene in age. Two existing species, *Terebratula sinuosa* (Brocchi) and *T. calabra* Seguenza, are placed in synonymy with *T. terebratula*. Three species are currently recognised in *Terebratula*, ranging in age from Miocene to Early Pleistocene when the genus became extinct, probably because of ocean cooling in the Mediterranean region.

## INTRODUCTION

The brachiopod genus *Terebratula* has a long and complex geological and nomenclatural history. The nominal genus *Terebratula* was proposed by Müller in 1776, and as pointed out by Muir-Wood (1955), it 'is the first valid post-Linnean brachiopod genus'. *Terebratula terebratula* (Linnaeus) is the name-bearer for the Order Terebratulida which encompasses loop-bearing brachiopods of Devonian – Recent age and includes most brachiopods living today.

The name *Terebratula* has been widely used for over 200 years: more than 850 specific names were applied to the genus between 1800–1850 alone (Sherborn, 1932). In spite of the ubiquity of the name, the genus and species on which it was originally based have, until recently, been little studied and many basic questions about *Terebratula terebratula* remained unanswered. As pointed out nearly a century ago (Buckman, 1907), not only was the type species of the genus unconfirmed, but its type locality and age were uncertain.

The present study had several aims. The first objective was to ratify the type of the genus *Terebratula* for inclusion in the revised Brachiopod *Treatise*, following the recommendation made by Muir-Wood in the 1965 *Treatise* volume on the Order Terebratulida. Secondly, we wished to summarise the complex nomenclatural history of the genus and species, *Terebratula terebratula*, since it was first illustrated and described in 1616. The third aim was to locate the type specimen and/or type locality of *T. terebratula*, or, if this proved impossible, select a neotype to act as namebearer for the order. Finally, we wished to describe the age and relationships of species currently included in *Terebratula*.

The first objective was achieved with an application to the International Commission on Zoological Nomenclature to validate the selection of *Anomia terebratula* Linnaeus as type-species of the genus *Terebratula* as designated by Lamarck in 1799 (Lee & Brunton, 1998; Ruling of the Commission, September 2000). The remaining objectives are achieved in this paper.

## DERIVATION OF THE NAME

The name *Terebratula* was first used in print by Lhwyd (1699) (Little *et al.*, 1973), and is the oldest generic name in the Phylum Brachiopoda in current use. *Terebratula* is 'so-called from the perforated beak of the ventral valve' (Little *et al.*, 1973: 2265), and is a quasi-diminutive of Latin *terebratus*, the past participle of *terebrare* 'to bore'. The brachiopods listed as *Terebratula* in Lhwyd's catalogue of shells in the collections of the Ashmolean Museum, Oxford, were 'poorly figured specimens from Witney' (Muir-Wood, 1955: 2). The name came into fairly common use in the 18th century, and some of the numerous brachiopods referred to as *Terebratula* by other pre-Linnean authors were mentioned by Muir-Wood (1955).

The species name *terebratula* was first used in a valid binomial by Linnaeus in his description of *Anomia terebratula* in Systema Naturae (1758: 703). Linnaeus gave no illustration, but referred to figures in Colonna (1616c), Lister (1678) and Klein (1753). The Colonna, and Colonna/Klein, illustrations are reproduced in Figs 1, 2.

## THE COLONNA ILLUSTRATION OF *TEREBRATULA* (FIG. 1)

Fabio Colonna (1567–1650) (Fabius Columna) was born in Naples and was one of the first natural historians to use copper plates for engraving botanical and zoological figures. He wrote extensively on
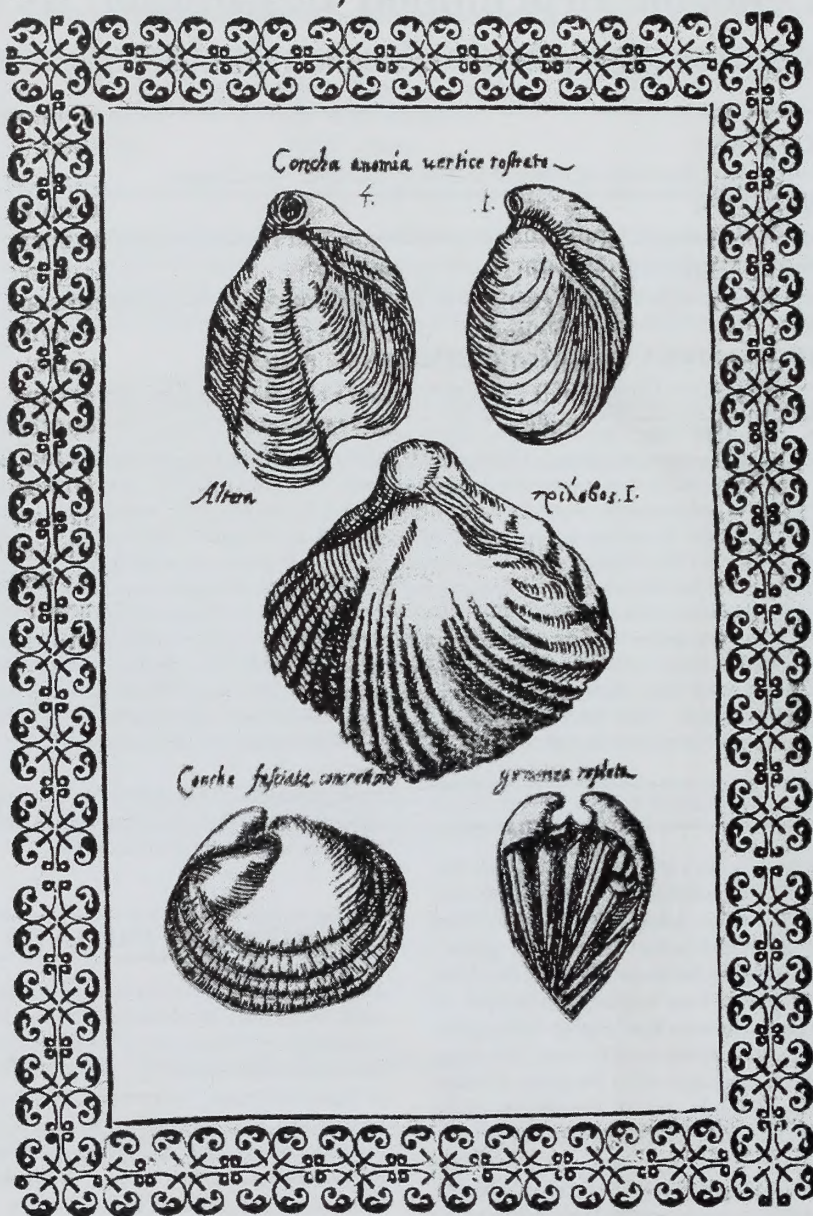
## 22    Fabij Columnæ



**Fig. 1**   Reproduction of page 22 in *Purpura* (Colonna, 1616).

fossils, and 'was one of the first to place them . . . in a primarily biological context . . . Colonna also applied the same precise nomenclature to his fossils as to his living animals, distinguishing different kinds of related fossils with more accuracy then ever before' (Rudwick, 1985: 42).

Colonna was a member of the Accademia dei Lincei (Academy of Lynxes), and in 1606, he published a work on natural history: *Minus cognitarum stirpium aliquot, ac etiam rariorum nostro coelo orientium [ecphrasis] . . De aquatilibus, aliisque animalibus quibusdam paucis libellus [plants pp.3–340; animals I–LXXIII]*. A new edition was published in 1616 (Colonna, 1616a–c), including part III, *Purpura* (of which *De purpura, aliisque testaceis rarioribus,*

pp. 1–29, and *De glossopetris dissertatio,* pp. 31–39, are two chapters), in which he described and figured a number of shells, some fossil and some living. His illustration on page 22 (Fig. 1 herein) was a woodcut of five shells. The upper three specimens are double-valved brachiopods, while the lower specimens are internal molds of bivalves. The plate is not numbered, and the five specimens are distinguished by brief captions placed above each specimen.

Linnaeus (1758: 703) made three separate references to the illustrations of brachiopods on this plate in his discussion of species of *Anomia*. Under *Caputserpentis*. 200., he gave a brief description, and referred to Column. purp. 22. f.2, i.e. the smooth brachiopod on the upper right. Brunton & Cocks (1967) discussed in detail the
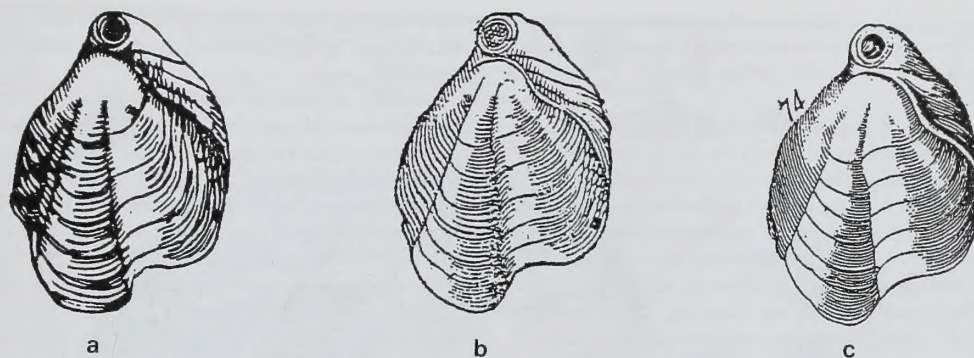
**Fig. 2** Figures of *Concha anomia*, the holotype of *Anomia terebratula*. **2a,** woodcut from Colonna (1616); **2b,** woodcut from Major (1675); **2c,** engraving from Klein (1753).

ambiguities which arose when Linnaeus (1767) changed his description of *A. caputserpentis* from a smooth, fossil brachiopod to a capillate living species (now *Terebratulina retusa*), although he retained the reference to the Colonna figure. An application to the International Commission on Zoological Nomenclature to change the type species of *Terebratulina* d'Orbigny, 1847 from *Anomia caputserpentis* Linnaeus, 1758, to *Anomia retusa* Linnaeus, 1758, disposed of the ambiguity caused by Linnaeus himself when he altered his definition of *A. caputserpentis* between 1758 and 1767 (Brunton & Cocks (1967: 295); Ruling of the Commission, 1968).

Under *Terebratula*. 201., Linnaeus listed three separate illustrations. The first, 'Column. purp. 22. f.1', refers to the upper left figure of a smooth, strongly folded brachiopod. The second refers to 'List. angl. 240.t. 8. f. 46', which is a non-plicate Jurassic shell from England (Lister, 1678). The third reference, which confirms that Linnaeus did indeed intend the upper left brachiopod to be the type of *terebratula*, is unmistakably the same (redrawn) Colonna illustration reproduced in a figure by Klein (1753) (Fig. 2 herein). Buckman (1907: 528) pointed out that Lister's figure did not match the description given by Linnaeus, and that the Colonna-Klein figure 'must be taken as the holotype, which, in fact, has been the usual practice'.

Linnaeus included the central figure in Colonna's plate in his '*Hysterita*. 203. Mus. Tess. 90. t.5.f.1,2,2. Column. purp. 22. f. 3? Trilobos.' This large, strongly ribbed and folded fossil rhynchonellid does not correspond to the *Mus. Tess.* illustration listed by Linnaeus, which is an internal mold of *Schizophoria* (Brunton *et al.*, 1967).

The two upper brachiopods in the Colonna figure are both smooth terebratulid brachiopods with large open foramens and strongly delineated growth bands. Across both drawings is the caption: '*Concha anomia vertice rostrato*', and beneath the left figure, although probably relating to the central brachiopod on the plate, is the word *Altera* (another). On the adjacent page 23, in *Purpura*, the chapter is headed *Concha rarior Anomia vertice rostrato. I. Cap. XII* (or 'rare Anomia shell with apical beak'). Although there is no scale on the illustration, the brachiopod on the upper right is at natural size (*icon magnitudinem aequat* on page 23 in *Purpura*).

## CONCHA ANOMIA VERTICE ROSTRATO

Some of the problems which have made it difficult for earlier and present authors to define *Terebratula* arise from the lack of correspondence between the figures on page 22 of Colonna, and the text

on the following pages. In particular, several specimens mentioned on pages 23–24 are not illustrated at all, although they were numbered sequentially by the author.

Thus, Lee & Brunton (1998) assumed that the strongly folded figure on the upper left on page 22 was that described in the text on the facing page (Cap. XII) under the heading '*Concha rarior Anomia vertice rostrato*', and accordingly they concluded that this specimen was that collected by Colonna from Andria. More recently, we have found that this might not be correct. In five original copies of Colonna's *Purpura* (1616c) held by the University of Naples 'Federico II' (two in the Library, and three in the Department of Biologia Vegetale and the Botanical Garden) and in another original copy held in the Botany Library of the Natural History Museum, London, the two figures at the top of page 22 are marked with '4' (upper left), and 'I' (upper right). These small numbers are not shown in the two published reproductions of Colonna's plate (Dollfus & Dautzenberg, 1932; Muir-Wood, 1955), nor in the 1675 edition of Colonna's *Purpura* edited by Major.

The following section attempts to clarify the problems we have encountered.

1. Colonna described four *Conchae* in the text on pages 23–24 and marked them with a Roman or Arabic notation. Of these, only the first (I) and the fourth (4) are figured on page 22. The four *Conchae* are:

   (i) ***Concha rarior Anomia vertice rostrato.*** I. Cap. XII ('I' on page 22 and 'I' on page 23). The description of 'I' corresponds to figure 'I' (page 22, top right).

   (ii) ***minor 2*** ('2' at the edge of the margin of line 29 on page 23). This specimen is not figured by Colonna.

   (iii) ***Altera Neptunia maior III. imbricata.*** Cap. XIII ('III' on page 24). This specimen is not figured by Colonna.

   (iv) ***Concha Anomia IV. margine undosa.*** Cap. XIV. ('4' on page 22 and 'IV' of page 24). The description of 'IV' corresponds to figure '4' (page 22, top left).

2. The first shell, (that is the smooth, unfolded specimen on the upper right on page 22) comes from Andria. The third comes from Nettuno (50 km south of Rome). The second and the fourth come from the Museum of Ferrante Imperato in Naples and their provenance is not given.

3. Colonna thought the four *Conchae* (ie., the figured and unfigured specimens described on pp. 23–24) were similar to each other. Indeed, in the index on p. 41 three of these are included under a single name '*Concha anomia quae, rarior vertice rostrato Plin.*

*descript. 23. icon. 22. Altera imbricata. 24. altera margine undosa, ibid. & 25'*. The two figures on the top of page 22 are joined under the same caption '*Concha anomia vertice rostrato*'.

The figure in the centre of page 22, described on pages 24–25 as '*Concha altera Anomia striata [trilobos] rarior. I. Cap. XV.*', is considered as another shell and its numeration starts again from 'I'.

Much of the confusion over the identity of the two figures on the top of page 22 stems from the fact that Colonna described the shell placed on the upper right first, and on a following page discussed the shell portrayed on the upper left, using a different practice from that which became well established in the following centuries. The confusion increased further when later authors assigned to these figures two numbers that Colonna had never employed. Thus Linnaeus (1758), following modern convention, designated the strongly folded specimen on the upper left as f. 1 (ie., figure 1) and that on the upper right as f. 2 (ie., figure 2). Brocchi (1814), and the present authors, until lately, have done the same.

The problem of deducing which shell description accompanied which illustration was compounded in a second edition of Colonna's work, with the associated text from the earlier edition subdivided into numbered paragraphs, which was reprinted posthumously in 1675 by J.D. Major. In this edition, the redrawn figure of the strongly folded specimen from the upper left of page 22 in the 1616 edition (i.e. *Anomia terebratula* of Linnaeus) appeared on page 32 within the text referring to the Andria locality. Similarly, in the Dictionarium this figure was noted by Major as that described in Cap. 12, of Colonna (1616c: 23).

A comparison of the three figures (Fig. 2 herein) shows that the Klein figure listed by Linnaeus (Klein, 1753; Tab. Nostra XI. n. 74), was redrawn from this later edition (Major, 1675) (Fab. Columnae de Purp. Cap. XII $.3. pag. 32 [Klein 1753, p. 171–2]).

Dollfus & Dautzenberg (1932) correctly interpreted the references to Major's figures, but added to the confusion, by giving the same citation for both the upper right and upper left figures: ie. 'p. 22, fig.1 (2e)'. These authors also assumed that the caption '*Altera*' pertained to the upper left figure, whereas it undoubtedly refers to the figure in the center ('*Altera [trilobos]*'), because the captions in all seven figures in Colonna's *Purpura* (pp. 13, 16, 20, 22, 27, 30, 33) are placed over, and never under, the relevant figures.

## DISCUSSION AND COMMENTS

This discovery, as our manuscript was almost ready for submission and after the ICZN had approved the selection of a neotype for *Terebratula terebratula* (Linnaeus), raises some issues which need further discussion. If indeed the provenance of the specimen selected by Linnaeus as the type of *Anomia terebratula* is unknown and the specimen is lost, then the basis for the species, and consequently the genus, family and superfamily would remain uncertain.

However, since Lee & Brunton (1998) have already nominated a neotype from Colonna's locality near Andria, the neotype locality now becomes the type locality for the species, regardless of the locality of the original Colonna brachiopod (International Code of Zoological Nomenclature Article 75f).

Is it possible then to determine the provenance of the original specimen of Colonna selected by Linnaeus as the type of *Anomia terebratula*?

Firstly, it is obvious that Colonna's caption: '*Concha anomia vertice rostrato*' applies to both of the brachiopods figured on the upper right and upper left of page 22, the first of which (that on the

upper right) certainly came from Pliocene strata near Andria, and that Colonna himself regarded these specimens as similar to one another.

Secondly, six original copies of Colonna (1616c) that we have consulted have the numbers:'I', '4' and 'I' written beside the three brachiopods figured on page 22. These numbers are not included in Major's edition. Linnaeus (1758, 1767) and Brocchi (1814), if aware of these numbers, used different, modern numbering (i.e. f.1 for Colonna's specimen 4 on the upper left), and Major (1675) and Lee & Brunton (1998) considered that Colonna's description on page 23 referred to the figure on the upper left.

Thirdly, even if the specimen of Colonna's (1616c: 22) upper left figure is from an unknown locality, it was filled with white, loose sediment (Colonna, 1616c: 24), and it is possible that it was collected from the same Pliocene calcarenites at Andria.

From a close examination of the Colonna woodcut, it seems likely that his specimen was somewhat deformed. It has a large, open foramen, and two strongly developed plicae/folds on the dorsal valve that begin at an early stage of growth, and would have resulted in a strong sulciplication (*margine undosa*) of the anterior commissure. The artist (?Colonna himself) may have exaggerated the depth of the folds, although the depiction of the other brachiopods on the plate seem to be faithful to reality. No undeformed specimens collected by the authors have folds as strongly developed as those depicted in the woodcut.

From the many specimens of *Terebratula* collected by the authors from Colonna's Andria locality and from elsewhere in Italy, it is apparent that the brachiopods in any fossil assemblage/population vary considerably in the degree of folding and may be rectimarginate to biplicate or sulciplicate. Thus, both specimens labelled by Colonna as *Concha anomia vertice rostrato* are species of *Terebratula* (*sensu lato*), and given the wide variation in populations of Neogene *Terebratula*, might be conspecific. Certainly, the specimens of *Terebratula terebratula* figured by us in this paper (Figs 6–9) fall somewhere in the middle of the two short-looped brachiopods illustrated in Colonna's woodcut. The specimen of Pliocene *Terebratula terebratula* from Monte Mario selected and figured by Buckman (1907) and illustrated in the 1965 *Treatise*, is crushed and deformed in a similar manner. In the Natural History Museum, London, there are several collections of *Terebratula* from this same horizon at Monte Mario, near Rome. These specimens, which are almost certainly conspecific, vary from small rectimarginate (juvenile) specimens (labelled *T. depressa*) to large rectimarginate individuals (named *T. grandis*), to examples with moderate sulciplication (labelled *T. ampulla* or *T. terebratula*).

Thus, our selection of a neotype from a locality described and collected by Colonna closely follows the recommendations of the Code.

It should be noted that Muir-Wood's (1955: fig. 2) caption for her reproduction of the original Colonna figure is misleading. The caption reads 'Reproduction of early drawings of Brachiopods figured as '*Concha anomia*', and taken from Fabio Colonna's first edition of *de Purpura*, 1616, p. 22. The first figure is of a specimen from Mte. Mario, near Rome, and is probably of Tertiary (?Pliocene) age; the other two figures may represent Jurassic forms'. However, as shown here, the first figure is from an unknown locality, while the second specimen is of Pliocene age and came from near Andria, not Rome.

## TYPE LOCALITY OF *TEREBRATULA TEREBRATULA*

Colonna (1616c: 23) described the locality from which he collected his specimen of *Terebratula* shown on the top right of his figure
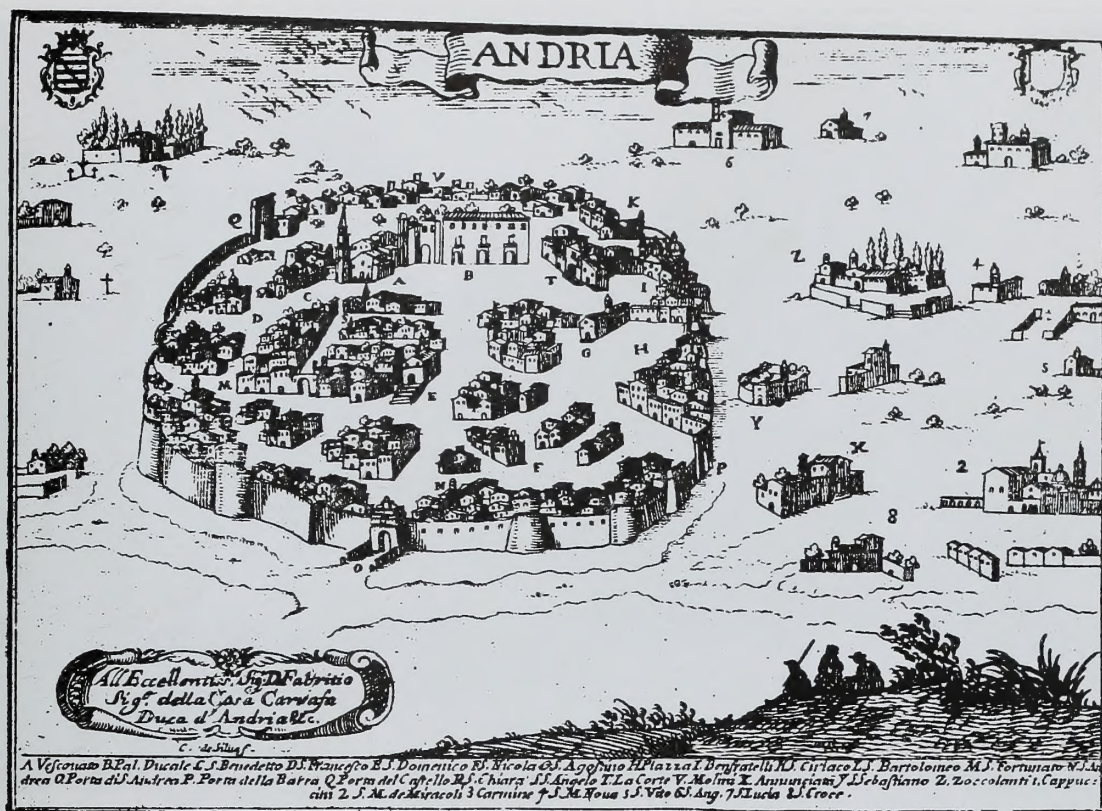
**Fig. 3** Reproduction of Pacichelli's late 17th century map of Andria. North is at the bottom of the figure, and the church of Santa Maria dei Miracoli (2 in the key) is west of the city near the right hand edge of the map.

(Colonna, 1616: 22) as follows: 'We found this shell full of the white sediment [`tophacea concretione'] on which that whole sloping area or hill is made. This is constituted not so much of loose sediments, as of fragments of various shells and unbroken shells too. We collected this one and others in the small valley or ditch a little below the Church of D. Maria de Andria, which is situated one mile outside the city' (see the Appendix for a translation of Colonna's pp. 23 and 24).

In the modern town of Andria the names of five churches include the word 'Maria', and to find which of them was the one referred to by Colonna it was necessary to consult Pacichelli's late seventeenth century map of Andria (Fig. 3). The churches of Santa Maria Nova (4 on Fig. 3) and Santa Maria dei Miracoli (2 on Fig. 3) are both situated outside the town to the west (west is on the right hand side of Fig. 3), but only the latter church is built directly on the `tophacea concretione' (= Calcarenite di Gravina Formation). On either side of a small natural valley (now dry) adjacent to the church of Santa Maria dei Miracoli 1–3m high cliffs of white, well-cemented calcarenite outcrop sporadically (Fig. 4), and specimens of *Terebratula* are scattered throughout the calcarenite showing that this locality is undoubtedly the one visited by Colonna. The brachiopods are not uncommon, but are often fragile and/or broken.

The basement rocks of the region around Andria are Lower Cretaceous in age. Overlying these with angular unconformity are 25 to 30m of coarse-grained highly fossiliferous marine biocalcarenites and calcirudites of the Calcarenite di Gravina Formation which is widespread in this area. In the vicinity of the Madonna d'Andria church, the sequence consists of 2m of fine, bioturbated, massive calcarenites lacking macrofossils. Above this is a coarse, bioturbated calcarenite up to 4m thick which includes

oysters, scattered pectinids, echinoids and brachiopods (Fig. 5). The upper 2m thick bed is a well-cemented, very fossiliferous calcarenite with a discontinuous oyster bed near its base. Fossils include *Ostrea*, *Chlamys*, internal moulds of bivalves such as Veneridae, echinoids, calcareous algae and brachiopods.

On macrofossil (Caldara, 1987; Caldara & Gissi, 1993) and microfossil (Taddei Ruggiero, 1996) evidence, the lower part of the Calcarenite di Gravina Formation is locally Middle to Upper Pliocene, or possibly Upper Pliocene to Lower Pleistocene in age. No trace of a cool-temperature Pleistocene macrofossil fauna was found during our visit.

Thus, the type locality for the neotype of *Terebratula terebratula* (Linnaeus) is adjacent to the church of Santa Maria dei Miracoli, about 2 km west of Andria, Puglia, Italy in the Calcarenite di Gravina Formation, of Upper Pliocene age. The specimen selected as neotype comes from beneath a small overhang about 200 m north of the church. The outcrops are difficult to access, and involve crossing private property.

## SYSTEMATIC DESCRIPTIONS

Order **TEREBRATULIDA** Moore, 1952
Superfamily **TEREBRATULOIDEA** Schuchert, 1913
Family **TEREBRATULIDAE** Gray, 1840

DIAGNOSIS. Medium to large, ventribiconvex, rectimarginate to uniplicate or biplicate, rarely unisulcate or sulciplicate, smooth or

**Fig. 4**   Outcrops of the Calcarenite di Gravina Formation, from which the neotype was collected, in the small valley north of the church.
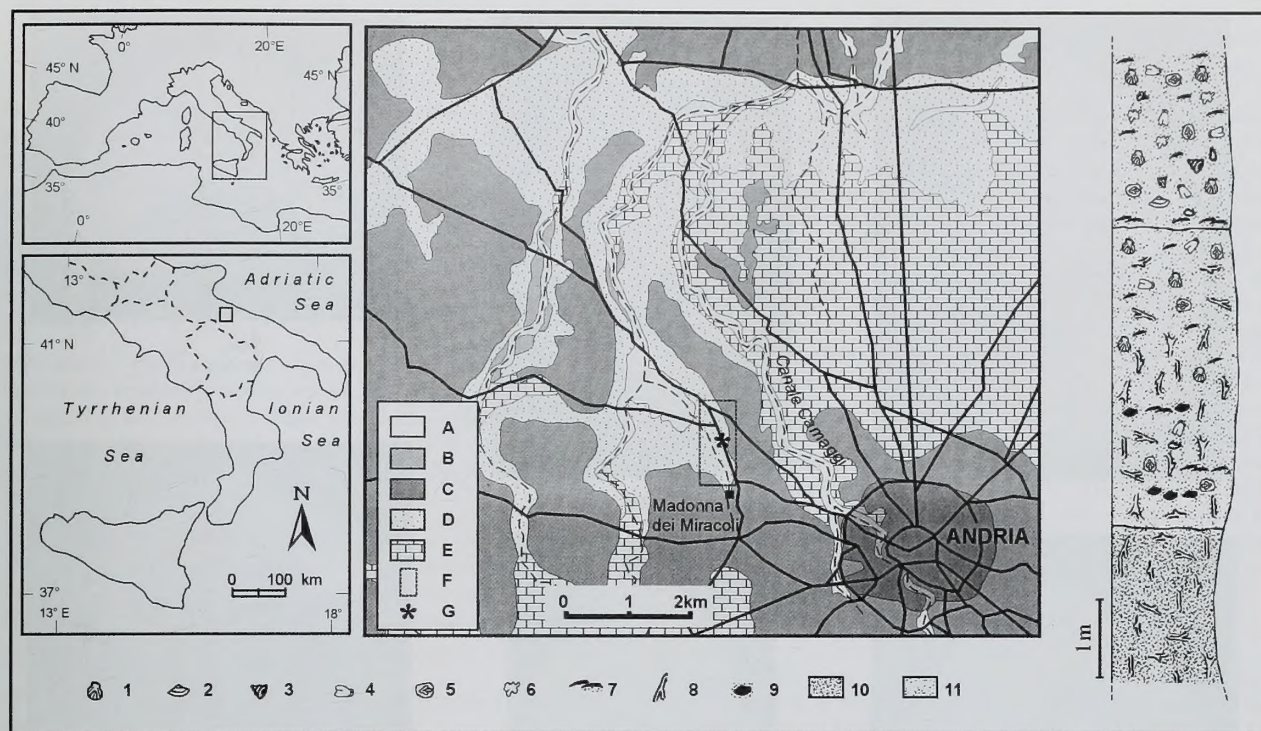
**Fig. 5** Location map, geological map and stratigraphic column for the Andria region, Puglia, Italy. **A,** alluvial deposits (Holocene); **B,** terraced alluvial deposits (Pleistocene); **C,** terraced marine deposits (Pleistocene); **D,** Calcarenite di Gravina Formation (Upper Pliocene); **E,** Calcare di Bari Formation (Lower Cretaceous); **F,** Colonna's locality; **G,** outcrop from which the neotype of *Terebratula* was collected (see stratigraphic column). **1,** Pectinidae; **2,** Veneridae; **3,** gastropods; **4,** brachiopods; **5,** echinoids; **6,** calcareous algae; **7,** oysters; **8,** bioturbations; **9,** mud pebbles; **10,** fine calcarenite; **11,** coarse calcarenite.

with fine radial capillae; loop short, triangular; outer hinge plates usually concave or flat, commonly attached to dorsal edge of crural base, inner hinge plates rarely developed.

### Subfamily TEREBRATULINAE Gray, 1840
### Genus *TEREBRATULA* Müller, 1776: 249

DIAGNOSIS. Medium to large, subpentagonal to broadly oval, smooth; anterior commissure rectimarginate to uniplicate or sulciplicate; beak short, erect; foramen large, symphytium partly visible. Pedicle collar short; cardinal process flat and semielliptical to a thickened boss; outer hinge plates narrow or lacking; crural processes may be long; loop short, broadly triangular; transverse band narrow, forming a low arch.

TYPE SPECIES. *Anomia terebratula* Linnaeus, 1758, by the subsequent designation of Lamarck (1799: 89).

GEOGRAPHIC RANGE. Italy, Sicily, Malta, Spain, Algeria.

STRATIGRAPHIC RANGE. Miocene – Early Pleistocene.

REMARKS. The great majority of the thousand or more specific names attributed to *Terebratula* have long been accommodated in other genera. However, although *T. terebratula* is the oldest available name for the medium to large, smooth, short-looped Miocene – Pleistocene terebratulids from Italy and the circum-Mediterranean region, it has rarely been used in the literature or in identification of specimens for the reasons outlined above. This is due mainly to the

uncertainties surrounding the identity, age and type locality of the Colonna specimen. The Colonna work is rare, and no translation has hitherto been available. Secondly, there was doubt as to the correct type species for the genus.

Gaetani & Saccà (1985), in a paper dealing with systematics and shell structure of brachiopods of Miocene – Pleistocene age from southern Italy, commented on the problem of recognising *T. terebratula*. They concluded that there were two valid species: *Terebratula sinuosa* (Brocchi) and *T. calabra* Seguenza which were restricted to the Upper Miocene and Pliocene respectively. Cooper (1983) identified large sulciplicate specimens of Pliocene age from Monte Mario, Rome, as *T. ampulla*. Other authors (Taddei Ruggiero, 1986, 1990, 1994, 1996) have identified large, shellbed-forming Pleistocene specimens as *T. scillae* Seguenza. Until variation within large populations of the species placed in *Terebratula* has been studied, we are able to recognise only three valid species of *Terebratula* – *T. terebratula* (Linnaeus, 1758), *T. ampulla* (Brocchi, 1814) and *T. scillae* Seguenza, 1871.

### *Terebratula terebratula* (Linnaeus, 1758)  Figs 6–9

1758 *Anomia terebratula* Linnaeus: 703.

SYNONYMS
1. *Anomia sinuosa* Brocchi, 1814: 468, is an objective synonym because Brocchi gave no figure, but referred to 'Column. 22, f.1', which is the holotype of *Anomia terebratula*.
2. *Terebratula calabra* Seguenza, 1871: 64
3. *Terebratula costae* Seguenza, 1871: 67; Taddei Ruggiero, 1994: 206.

**Figs 6–9**  Neotype and 3 topotypes of *Terebratula terebratula* (Linnaeus) from a Colonna locality at Madonna dei Miracoli, Andria, Italy. **6a–c,** dorsal, lateral and anterior views of neotype, NHM BG152 (length 55.4mm); **7a–c,** dorsal, ventral and anterior views of topotype, NHM BG194 (length 50.8mm); **8a, b,** ventral and anterior views of topotype, NHM BG195, showing M-shaped anterior commissure; **9a, b,** ventral views of loop of topotype, NHM BG196. All figures natural size, except Fig. 9b.

TYPE SPECIMENS.    The holotype, the specimen figured by Colonna (1616c), is lost. We here nominate as neotype (Fig. 6a–c), an entire specimen from the Calcarenite di Gravina Formation near a locality collected by Colonna, in the collection of the Natural History Museum, London (BMNH BG152), collected 22 March 1998 by M. Caldara & O. Simone. Dimensions of the neotype are: length 55.4 mm, width 43 mm, thickness 30mm. A well-preserved complete topotype with the dimensions: length 50.8 mm, width 42 mm, thickness 28 mm, is also figured (Figs 7a–c). Two further topotypes, one with a complete loop (Figs 9a, b), and a dorsal valve with a strongly-M-shaped anterior commissure (Figs 8a, b) are also illustrated.

MATERIAL.    The brachiopods from the Calcarenite di Gravina Formation are frequently broken across mid-valve, or are separated valves. Most specimens are infilled with coarse, white, hard, moderately cemented calcarenite, and few have a complete anterior commissure. A number of topotypes (BG153–161, BG194–196) are held in The Natural History Museum, London.

TYPE LOCALITY.    The type locality is an outcrop of Calcarenite di Gravina Formation, of Pliocene age, on the east side of a small dry valley, about 200m north of the church of Madonna dei Miracoli (41°13'52"N; 16°16'00"E), about 2km west of Andria, Puglia, Italy.

AGE.    Late Miocene (Tortonian), Pliocene.

DISTRIBUTION.    Puglia, Calabria, Tuscany, Emilia (Piacentino), Abruzzi, Spain (Alicante).

DESCRIPTION.    Shell of medium to large size, biconvex, anterior commissure rectimarginate, uniplicate to sulciplicate, two broad plicae may be developed; beak short, massive, suberect; foramen large, mesothyrid to permesothyrid; symphytium narrow, partly concealed. Pedicle collar short; hinge teeth with moderately swollen bases. Cardinal process semielliptical, moderately protuberant; outer hinge plates narrow; no inner hinge plates; crural bases fused to socket ridges to form a deep V-shaped trough, crural processes long; loop broadly triangular, about 0.3 valve length, transverse band narrow, forming medially flattened low arch.

### *Terebratula ampulla* (Brocchi, 1814)

1814    *Anomia ampulla* Brocchi: 466

AGE.    Pliocene.

DISTRIBUTION.    Italy (Emilia (Piacentino), Tuscany, from Brocchi's list), but not Calabria (see Seguenza, 1871).

COMMENTS.    A medium-sized, strongly bisulcate species.

### *Terebratula scillae* Seguenza, 1871

1871    *Terebratula scillae* Seguenza: 39

AGE.    Early Pleistocene.

DISTRIBUTION.    Calabria, Puglia, Sicily.

COMMENTS.    The largest species of *Terebratula* (up to 95mm in length), which formed extensive shellbeds in the Early Pleistocene.

## ECOLOGY AND EXTINCTION OF *TEREBRATULA*

*Terebratula grandis* Blumenbach, 1803, now included in the genus *Pliothyrina* (see Cooper, 1983), may be the ancestor of *Terebratula*

*sensu stricto*. This large species from the Oligocene of Germany needs further study. *Pliothyrina* appears to have been widespread in northern Europe and England (see collections in the Natural History Museum, London), whereas *Terebratula* was abundant in the Mediterranean region. Both groups became extinct in the Plio-Pleistocene.

*Terebratula* was widely distributed in the Mediterranean region from the Miocene until the early Pleistocene. It lived in circalittoral environments on muddy, biodetrital seafloors, attached to substrates which included bivalves and other brachiopods. During the Messinian, when the Mediterranean basin became too saline to support normal marine life, the brachiopod fauna disappeared from the region. With flooding of the Atlantic sea into the Mediterranean basin, the Mediterranean was recolonised by a brachiopod biota with Atlantic affinities (Logan, 1979). This does not account for the reappearance of *Terebratula*, which may have survived in refugia.

In the Pliocene, *Terebratula* was an important component of a widespread brachiopod fauna which included *Aphelesia* and *Megerlia* (Gaetani, 1986; Taddei Ruggiero, 1994, 1995). The youngest records are of very large *Terebratula scillae* which formed vast shellbeds in the Early Pleistocene (Taddei Ruggiero, 1986, 1994). The extinction of *Terebratula* by the Middle Pleistocene appears to be related to the reduction in sea temperatures as Pleistocene cooling proceeded.

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# APPENDIX

Translation of Colonna, 1616c, page 23 and part of page 24, provided by Professor John Barsby, Department of Classics, University of Otago, and Professor Roberto Taddei, Dipartimento di Biologia Vegetale, Universita' di Napoli 'Federico II'.

### Page 23, Concha rarior Anomia vertice rostrato. I. Cap.XII.

'Now we will discuss the one found in the city of Andria. If anyone of greater curiosity would seek them in that place, he will find many of the more rare ones, still unrecognised and unseen. And he will notice that nature has had a lot of fun in forming them. The appearance of this [shell] is smooth, depressed, a little elongated (longer than broad), differing from other shells especially in the fact that one of the two valves is longer and that it extends its umbo and the whole apex which is longer and rounder and sharper and sticks out above the apex of the other valve, so that the last apex is connected beneath the umbo of the first one. The shell is small, white, thin, and a little bit wrinkled transversely by additions [=with the surface marked by growth lines], but not for that reason rough, but smooth. We found this shell full of the white sediment on which that whole sloping area or hill is made. This is constituted not so much of loose sediments, as of fragments of various shells and unbroken shells too. We collected this one and others in the small valley or ditch a little below the Church of D. Maria de Andria, which is situated one mile outside the city. We were there to pay our thanks for favours received from most holy Mother of God, among the others who assemble there in great crowds every day to pay their vows. The church is adorned with large gifts and signs of miracles: the church itself has a sumptuous structure, as does the monastery. We observed one shell like this at the Museum of our very learned Imperato, a rich treasure of all natural things. This shell has a little sinuous margin and the longer valve has a slight groove in the back, another in the middle, protruding in opposite way (?). All the shells have the same particular feature, i.e. an orifice in the rostrate, prominent, apex, from which they can, as a turbine, suck and eject water, in the manner of a 'sylvester Lepas' or an 'Auris marinea'. The figure is natural size. A stony shell like this, but much greater, is figured in the first part, under the name Concha gibbosa.'

### Page 24, Altera Neptunia maior III. imbricata. Cap. XIII.

'Another twice larger, with sinuous margin too, we found in tufaceous or sandy materials near Albano, in which is the ditch of Castello (Castle) or Arce. And there are many different shells never complete, but all piled-up and tangled . . . The shell is 3 inches long, 2 wide, and in the middle has like another shell built on.'

### Concha anomia IV. margine undosa. Cap. XIV

'This differs from the previous similar one in the colour which is on the pale side, but was full of white, loose sediment too, for the wavy and curly margin so that it is like an 'M' letter, for the back is inflated and not hollow, because in the other valve a triple groove is recognisable, but all have a pierced apex. I had these, among the others, from the Museum of our Imperato.'

# Purpura. 23

### *Concha rarior Anomia vertice roſtrato . I. Cap. XII.*

ANomias Conchas illas eſſe dicimus , quarum altera pars co-
hærens aliquo modo ab altera effigie , aut magnitudine , aut
vtroque modo differat ἀνόμοις , quidem contrarium eſt verbi ὅμοιοῦ ,
quod eſt ,*ſimilis, par, æqualis,* ſcilicet , *diſſimilis, impar, inæqualis* : *Lib. 9. c. 35*
ideo inter ceteras notas à Plinio memoratas, quibus Concharum
varietates diſtinguit plurimas , cum inæqualitatis notam non inue-
nerimus , Anomias Conchas appellare libuit , vel Plinij more illas,
*vertice roſtrato,*dicere; quarum etiam differentiæ ſunt plures : Nunc
de hac in Ciuitate Andriæ reperta verba faciemus , in quo loco ſi
quis curioſior perquirere vellet, illas etiam rariores non paucas in-
ueniet adhuc incognitas , & inuiſas . Naturamq́; in his efforman-
dis multum luſiſſe animaduertet. Huius igitur effigies læuis,depreſ-
ſa,parum oblonga,ab alijs Conchis in hoc præcipuè differens ,quod
altera Conchæ pars oblongior eſt, collum, ceruicemq́; totam , quæ
oblongior eſt, & rotundior,atque acutior, prominetq́; ſupra cerui-
cem alterius diffundit , vt infra illius collum altera ceruix conne-
ctatur. Concha parua eſt, candida, tenuis , obliquè parum addita-
mentis rugoſa , ſed non ob id aſpera , ſed læuis . Repletam inueni-
mus candida tophacea concretione , qua totus ille cliuoſus locus ,
ſiue collis eſt editus, qui non magis terrena concretione tophacea,
quam variarum Concharum fragmentis, & integris etiam innume-
ris eſt compactus : hanc & alias in vallecula illa, ſiue foſſa quadam
parum ſubtus Eccleſiam D. Mariæ de Andria,extra vrbem miliario
ſita,excepimus : illic enim ob gratias à Sanctiſſima Dei Genitrice
acceptas referendas fuimus,ſicuti & alij magna cum frequentia vo-
ta ſoluentes concurrunt quotidie : Eccleſia quidem illa magnis do-
nis , & miraculorum ſignis ornatur,nec non ſumptuoſa ſtructura ip-
ſa Eccleſia, & Monaſterium . Huius ſimilem apud doctiſſimum Im- *minor 2.*
peratum noſtrum in ſuo Muſæo,rerum omnium naturæ ſatis copio-
ſo theſauro , obſeruauimus , quæ margine erat parum vndoſa , &
longiore conchæ parte canalem vix cóſpicuum in dorſo,altero verò
in medio,cótrario modo extuberante,omneſque peculiari nota ſūt
præditæ,quod ceruice prominente roſtrata,pertuſa oriuntur,qua tur
binatorum more aquam haurire & expuere, ſylueſtris Lepadis , aut
Auris marinæ modo poſſunt. icon magnitudinem æquat.Huic ſimi-
lem maiorem multo lapideam depinximus in prima parte,nomine
Conchæ gibboſæ .

*Altera*

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# 24 Fabij Columnæ

### *Altera Neptunia maior III. imbricata . Cap. XIII.*

DVplò maiorem alteram Neptuni reperimus Albanen. dio-
ceſis etiam vndoſa margine in tophaceis , ſiue ſabuloſis illis
concretionibus , in quibus Caſtelli ſiue Arcis foſſa eſt , & maxima
variarū teſtarū congeries conſpicitur , nec vnā reperies integram,
ſed omnes inter ſe congeſtas, & implicatas, vt non Natura,ſed ma-
ris impulſu fractas , & eiectas cum ſabulone , & molem illam to-
phaceā conſtruxiſſe teſtarū fragmentis repletā ſit cenſendum:quare
mare aliquando varijs in regionibus excreuiſſe & æſtuaſſe ſatis có-
ſtat,locaq́;immutata. Mirum quidem eſt huiuſinodi teſtas recentes,
& viuas hodie non reperiri , quamobrem è longè maris alluuione
profectas , & aduectas cenſemus potius , quam Naturam deſiſſe ſi-
miles parere.tres pollices longa,duos lata eſt teſta, habetq́; in me-
dio veluti alteram concham ſuper elatam imbricis modo,vt in alijs
obſeruatur, præſertim pectunculis .

### *Concha Anomia IV. margine vndoſa . Cap. XIV.*

DIffert hæc à ſuperiore congenere colore ad pallidum inclinan-
te, quæ etiam repleta erat concretione candida terrea , &
quod margine ſit vndoſa in ſpiras contorta , M, litteram repræſen-
tante , dorſumq́; habeat elatum , non cauum ; altera parte triplici
canali diſtinguatur,ſed omnes ceruicem habent perforatam,ex Im-
perati noſtri muſæo habuimus inter alias .

### *Concha altera Anomia ſtriata τριλοβος rarior. I. Cap. XV.*

EX eodem genere & hæc videtur,maior Concha,& craſſior;cu-
ius obeſa valua minor eſt,atque tribus ſimul iunctis teſtis,me
dia magis extuberante conſtructa videtur,& ſenis ſtrijs, totidemq́;
ſtrigibus in ſingulis lobis , quibus margines denticulatæ fiunt , inſe-
cta;præterquam pars interiecta interlobos,quæ recta linea marginē
definit . Altera parte, qua valuæ in caput prominet, medium habet
lobum depreſſiorem, & oblongiorem,reliquis à latere breuioribus,
& elatis , eodemq́; modo ſtriatis ; qua parte tota concha expanſis
alis auriculam incuruam repræſentare videtur Conchæ cortex ca-
ſtaneo

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**Fig. 10** Reproduction of Colonna, 1616c, pp. 23, 24.

XX (340021.1)

# Gough's Cave 1 (Somerset, England): a study of the pectoral girdle and upper limbs

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**SYNOPSIS.** The pectoral girdles, arms and forearms of Cheddar Man (Gough's Cave 1) are well preserved and, with the exception of a missing left scapula, are completely represented. These remains, which derive from early Holocene deposits in Gough's Cave, are described here. Comparative evaluation of the Gough's Cave 1 remains reveals that his upper limb skeleton was somewhat gracile, but certainly within the range of variation in strength measures of his contemporaries.

## INTRODUCTION

The upper appendicular skeleton of Cheddar Man is represented by both claviculae, the right-side scapula, the humeri, ulnae and radii of both sides, and elements of both hands. The preservation of the upper limb elements is generally good.

The elements of the pectoral girdles, arms and forearms are described below (the manual remains are described elsewhere), followed by a discussion of the overall morphology of the upper limbs.

## MATERIAL

The description of the Gough's Cave 1 upper limb remains includes both traditional osteometric (Tables 1, 2, 4–7, 9, 10, 12 and 13) and diaphyseal cross-sectional data (Tables 3, 8, and 11). Mean osteometric and cross-sectional data are provided for other European Mesolithic and later Upper Paleolithic specimens to provide a comparative framework for evaluating the morphology of Gough's Cave 1. These additional specimens range in geological age from the terminal Pleistocene to the mid-Holocene, and include Arene Candide 2 to 5, 10, and 12 to 15, Bruniquel 24, Cap-Blanc 1, Chancelade 1, Farincourt 1, Gramat 1, Hoëdic 1, 2, and 4 to 10, Neuessing 2, Oberkassel 1 and 2, Rochereil 1, Romito 3 and 4, Romanelli 1, St. Germain-la-Rivière 4, Téviec 1, 7 to 9, 11 and 16, and Veyrier 1 (Stasi & Regalia, 1904; Verworn *et al.*, 1919; Grazzini, 1921; Péquart & Péquart, 1934; Bonin, 1935; Boule & Vallois, 1937, 1946; Vallois, 1941–1946, 1972; Lacam *et al.*, 1944; Pittard & Sauter, 1945; Sauter, 1957; Graziosi, 1962; Genet-Varcin & Miquel, 1967; Billy, 1969; Gieseler, 1977; Paoli *et al.*, 1980). All comparative data were collected by the author on original specimens.

Diaphyseal cross-sections of the claviculae, humeri and ulnae were reconstructed from radiographs and external contour molds for the midshaft (claviculae and humeri) or mid-proximal (ulnae) diaphyses. Subperiosteal contour molds were taken perpendicular to the diaphyseal axis, using dental putty molds (Cuttersil Putty Plus: Heraeus Kulzer Inc.), at 50% (midshaft) or 65% (mid-proximal) of biomechanical length (measured from the distal end). The molds were photostatically reproduced on paper to provide the subperiosteal (outside) contour of the cross-section. In the case of claviculae, ventral, dorsal, superior and inferior cortical dimensions were measured from superoinferior and dorsoventral radiographs. For humeri and ulnae, anterior, posterior, medial and lateral cortical thicknesses were measured from mediolateral and anteroposterior radiographs.

Subperiosteal dimensions from the original specimens were compared with those from the radiographs to determine the degree of parallax distortion and thus allow for algebraic correction of cortical thickness measurements. The cortical dimensions were used along with the subperiosteal contour to interpolate the endosteal contour. The resultant cross-sections were manually digitized and geometric properties were computed using a PC-DOS version (Eschman, 1990) of SLICE (Nagurka & Hayes, 1970).

SLICE calculates the total subperiosteal (TA) and cortical (CA) areas, 2nd moments of area about the superoinferior (clavicle) or anteroposterior (humerus and ulna) ($I_x$) and dorsoventral (clavicle) or mediolateral (humerus and ulna) ($I_y$) axes, and the maximum ($I_{max}$) and minimum ($I_{min}$) 2nd moments of area. Geometric analysis of cross-sections provides measures of the contribution of bone geometry to the resistance of biomechanical loads: in the case of cortical area, to axial compressive and tensile loads; for 2nd moments of area, to bending loads. Medullary area (MA) can be determined from total and cortical areas (MA = TA – CA). The polar moment of area (J, or $I_p$) is a measure of torsional rigidity and overall strength, and can be determined as the sum of any two perpendicular 2nd moments of area (J = $[I_x + I_y]$ = $[I_{max} + I_{min}]$). Since cross-sectional measures of strength co-vary positively with body size, humeral and ulnar cross-sectional values were standardized by powers of bone length to produce measures of relative strength, or *robusticity*. Following the rationale described in Churchill (1994), measures of cross-sectional area (TA, CA and MA) were standardized as:

$$AREA_{standardized} = (AREA_{unstandardized}/AL^2) * 10^5$$

where AL = humeral or ulnar articular length. 2nd (and polar) moments of area ($I_x$, $I_y$, $I_{max}$, $I_{min}$, J) were similarly standardized as:

$$2nd\ Moment_{standardized} = (2nd\ Moment_{unstandardized}/AL^4) * 10^9.$$

In addition to the measures of bone rigidity outlined above, three cross-sectional shape indices were computed to better illustrate the morphology of the Gough's Cave 1 upper limb material. Percent cortical area (%CA = 100*CA/TA) serves as a simple measure of the degree of cortical occlusion of the medullary space. Ratios of 2nd moments of area provide information about diaphyseal shape (at the location of the cross section) with respect to anatomical axes ($I_x/I_y$) or with respect to the axis of maximum bending rigidity ($I_{max}/I_{min}$).

## CLAVICULAR REMAINS

Both claviculae are preserved and are virtually complete (Figs 1, 2). Both lack the sternal epiphysis but have well preserved metaphyseal plates, making it clear that the sternal secondary centres of ossification were unfused. The right clavicle is damaged on the inferior and
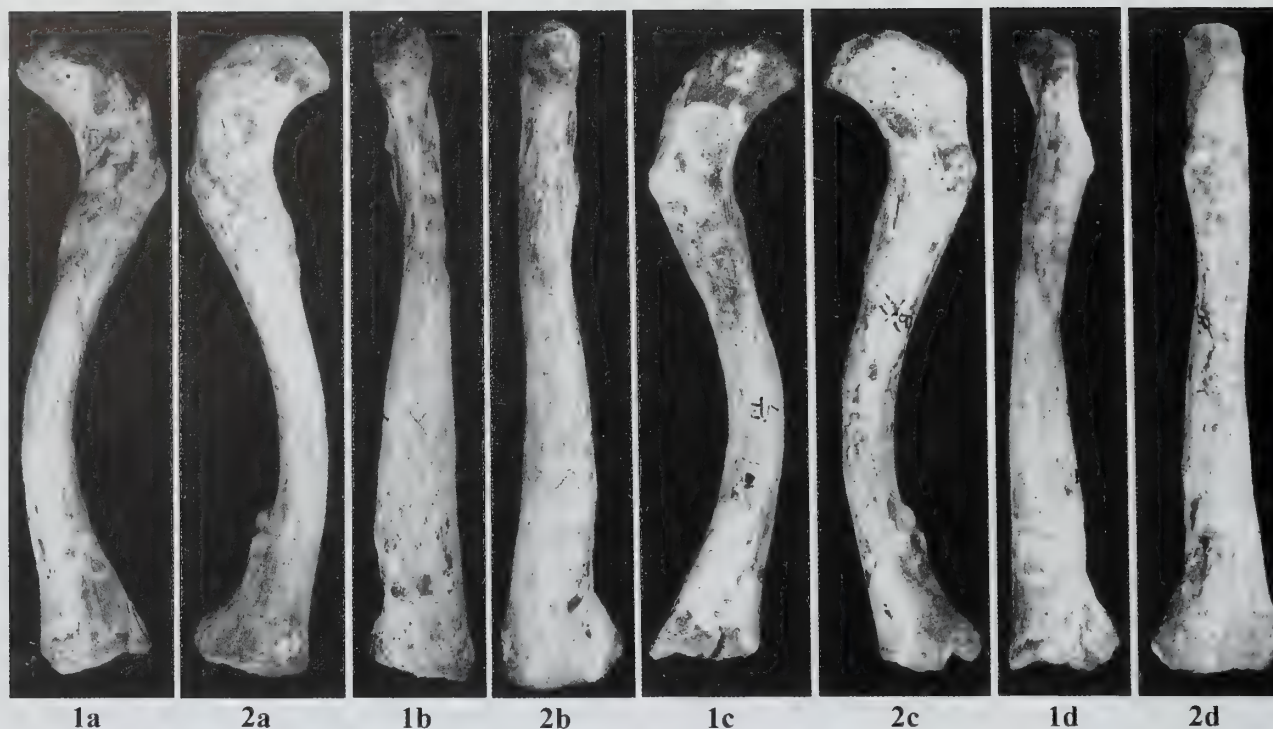
**Figs 1, 2**   Gough's Cave 1 claviculae, in superior (a), ventral (b), inferior (c) and dorsal (d) views; **1,** right-side clavicle; **2,** left-side clavicle; × 0.66.

dorsal aspects of the shaft around the costoclavicular ligament attachment area, and is patched with plaster in this location. The right-side bone also suffers from erosion and damage over the superior, dorsal and inferior surfaces of the acromial process. The left-side clavicle is undamaged.

Both claviculae are fairly short and stout and not markedly curved. The acromial ends are short and more curved than the proximal shafts, which have only a slight curvature. The sternal end of the right clavicle is round in medial view (with a maximum dorsoventral diameter of 20.9mm, and a maximum superoinferior diameter of 23.6mm), while the left is a dorsoventrally narrow oval (maximum DV diameter = 17.9mm, maximum SI diameter = 27.3mm). The right clavicle exhibits a greater degree of torsion in the shaft than the left clavicle. With the acromial processes held horizontally, in medial view the long axis of the articular surface (metaphyseal plate) of the right-side sternal end is inclined at a 45° angle (superoventral to inferodorsal) to the coronal plane. In the left clavicle, the long axis of the sternal articulation is also oriented superoventrally to inferodorsally, but it forms only a 15° angle with the coronal plane. The overall size and shaft curvatures is largely symmetrical between the sides (Table 1). The medial shafts are elongated superodorsal to inferoventral (*i.e.*, the long axes of the shaft cross-sections run in that direction).

The costoclavicular ligament attachment area (on the left clavicle, this area is obscured by plaster on the right clavicle) is a dorsoventrally narrow but mediolaterally long scar. The left-side costoclavicular ligament insertion area is dorsally placed, so much so that it is almost positioned on the dorsal surface of the shaft. On both sides the anterior medial shafts (in the vicinity of the *M. pectoralis major* attachment area) are flattened and are mostly smooth (there is some mild rugosity along the inferomedial edge of

**Table 1**   Dimensions (mm) of the Gough's Cave 1 claviculae.

|  | Right | Left |
|---|---|---|
| Maximum length (M-1)[a] | (135) | 135.9 |
| Articular length[a,b] | 128.3 | 132.2 |
| Conoid length[a,c] | 102.9 | 104.4 |
| Midshaft maximum diameter[d] | 13.9 | 13.9 |
| Midshaft minimum diameter[d] | 9.6 | 9.8 |
| Midshaft circumference (M-6) | 40 | 39 |
| Mid-proximal superoinferior diameter[e] | 14.6 | 11.4 |
| Mid-proximal anteroposterior diameter[e] | 12.3 | 12.6 |
| Mid-proximal circumference[e] | 42 | 40 |
| Proximal epiphyseal superoinferior diameter[f] | 23.3 | 26.4 |
| Proximal epiphyseal anteroposterior diameter[f] | 22.7 | 18.2 |
| Costal impression mediolateral diameter[g] | – | 19.5 |
| Costal impression dorsoventral diameter[g] | – | 9.5 |
| Conoid superoinferior diameter[h] | 12.7 | 13.5 |
| Conoid anteroposterior diameter[h] | 17.7 | 17.8 |
| Acromial superoinferior diameter[i] | 11.5 | 11.7 |
| Acromial anteroposterior diameter[i] | – | 21.5 |

Martin numbers (M-#: Martin, 1928) for measurements are provided where appropriate.
[a] length lacking the unfused sternal epiphysis.
[b] direct distance between the mid-points of the proximal and distal epiphyses.
[c] direct distance from the mid-point of the proximal epiphysis to the middle of the conoid tubercle.
[d] midshaft determined relative to articular length.
[e] taken at mid-conoid length.
[f] maximum (SI-superoinferior) and minimum (AP-anteroposterior) diameters of the proximal epiphysis.
[g] mediolateral and dorsoventral diameters of the costoclavicular ligament attachment area.
[h] taken at the conoid tubercle perpendicular (SI) and parallel (AP) to the superior surface of the bone.
[i] acromial diameters taken perpendicular (SI) and parallel (AP) to the superior surface of the bone.

**Table 2** Comparative clavicular osteometrics (mean, SD, n).

| | Gough's Cave 1 | LUP/Meso ♂ | LUP/Meso ♀ |
|---|---|---|---|
| *Right claviculae* | | | |
| Maximum length | (135) | 143.4, 6.4, 8 | 129.4, 2.7, 5 |
| Articular length | 128.3 | 138.2, 6.7, 8 | 126.3, 3.6, 5 |
| Conoid length | 102.9 | 110.7, 2, 10 | 100.4, 7.6, 7 |
| Mid-proximal SI diameter | 14.6 | 11.8, 1.7, 10 | 9.8, 0.5, 7 |
| Mid-proximal AP diameter | 12.3 | 11.7, 0.8, 10 | 10.3, 0.9, 7 |
| Conoid SI diameter | 12.7 | 12.6, 3.7, 10 | 9.8, 1.4, 10 |
| Conoid AP diameter | 17.7 | 17.7, 1.9, 10 | 15.2, 1.8, 10 |
| *Left claviculae* | | | |
| Maximum length | 135.9 | 145.4, 9.0, 10 | 128.0, –, 2 |
| Articular length | 132.2 | 140.6, 9.1, 10 | 125.6, –, 2 |
| Conoid length | 104.4 | 109.6, 9.8, 13 | 98.8, 5.4, 4 |
| Mid-proximal SI diameter | 11.4 | 11.8, 2.1, 16 | 10.0, 0.8, 6 |
| Mid-proximal AP diameter | 12.6 | 11.7, 0.8, 16 | 9.8, 1.3, 6 |
| Conoid SI diameter | 13.5 | 11.0, 1.7, 15 | 10.0, 1.1, 8 |
| Conoid AP diameter | 17.8 | 17.2, 3.0, 15 | 14.2, 1.3, 7 |

All measurements are in mm and are defined in Table 1.

**Table 3** Mid-shaft clavicular cross-sectional properties (mean, SD).

| | Gough's Cave 1 | LUP/Meso ♂ (n=4) | LUP/Meso ♀ (n=2) |
|---|---|---|---|
| *Right claviculae* | | | |
| Total area (TA) (mm$^2$) | 124.9 | 107.4, 8.0 | 68.8 |
| Cortical area (CA) (mm$^2$) | 87.3 | 84.0, 7.8 | 57.0 |
| Medullary area (MA) (mm$^2$) | 37.6 | 23.4, 7.2 | 11.8 |
| SI 2nd moment of area ($I_x$) (mm$^4$) | 1319.8 | 869.5, 198.1 | 450.9 |
| DV 2nd moment of area ($I_y$) (mm$^4$) | 1154.2 | 884.1, 96.2 | 305.4 |
| Maximum 2nd moment of area ($I_{max}$) (mm$^4$) | 1752.1 | 1001.2, 131.3 | 473.0 |
| Minimum 2nd moment of area ($I_{min}$) (mm$^4$) | 721.9 | 752.5, 139.5 | 283.3 |
| Polar moment of area (J) (mm$^4$) | 2474.0 | 1753.7, 264.2 | 756.3 |
| Percent cortical area (%CA) | 69.9 | 78.3, 6.1 | 82.9 |
| $I_x/I_y$ | 1.14 | 0.981, 0.185 | 1.487 |
| $I_{max}/I_{min}$ | 2.43 | 1.343, 0.113 | 1.690 |
| *Left claviculae* | | (n=4) | (n=3) |
| Total area (TA) (mm$^2$) | 118.9 | 122.0, 24.5 | 81.5, 17.9 |
| Cortical area (CA) (mm$^2$) | 73.9 | 91.2, 23.9 | 64.1, 13.1 |
| Medullary area (MA) (mm$^2$) | 45.0 | 30.8, 3.7 | 17.3, 5.1 |
| SI 2nd moment of area ($I_x$) (mm$^4$) | 999.6 | 1316.6, 671.8 | 559.3, 215.9 |
| DV 2nd moment of area ($I_y$) (mm$^4$) | 1084.4 | 1016.9, 325.7 | 498.9, 192.0 |
| Maximum 2nd moment of area ($I_{max}$) (mm$^4$) | 1505.1 | 1398.1, 626.5 | 591.6, 177.9 |
| Minimum 2nd moment of area ($I_{min}$) (mm$^4$) | 578.9 | 935.5, 364.1 | 466.7, 232.5 |
| Polar moment of area (J) (mm$^4$) | 2084.0 | 2333.5, 990.4 | 1058.3, 405.5 |
| Percent cortical area (%CA) | 62.2 | 74.2, 4.7 | 79.0, 2.2 |
| $I_x/I_y$ | 0.92 | 1.240, 0.307 | 1.127, 0.081 |
| $I_{max}/I_{min}$ | 2.60 | 1.468, 0.099 | 1.433, 0.517 |

See text for definition of measurements.

the *M. pectoralis major* origin area on the right-side bone; on the left-side there is some mild rugosity along the entire superior margin of the attachment area for this muscle). On the left clavicle there is a clearly defined insertion area for *M. sternocleidomastoideus*, beginning with a small but well defined projecting crest medially. This crest continues laterally as a narrow, mildly rugose strip extending about 25mm along the superior edge of the shaft. The right-side clavicle lacks a clearly marked insertion for *M. sternocleidomastoideus*, but instead has some poorly defined, mild rugosity in this area. On both sides, the *M. subclavius* attachment falls on a narrow ridge medially (between the *M. pectoralis major* origin area ventrally and the dorsal surface of the shaft dorsally) but broadens out as it nears the conoid tubercle on the proximal part of the acromial process. Here there is some mild rugosity (on the right, the left-side is largely non-rugose) and the attachment area is defined dorsally by a ridge

running to and joining the conoid tubercle. There is also a slight ridge, more prominent in the right clavicle, separating the *M. subclavius* origin area ventrally from the *M. deltoideus* attachment area. The area of origin of *M. deltoideus* is weathered and damaged on the right-side, but on the left it can be seen as a well defined, rugose and projecting crest.

The conoid tubercles are large and project both inferiorly and dorsally. Both have long ridges extending medially from the tubercles (these ridges form the dorsal margins of the *M. subclavius* attachment areas). The trapezoid line on the left clavicle (this area is damaged on the right clavicle) is not overly rugose but is clearly visible. The acromial facets are poorly defined. The *M. trapezius* attachment areas are rugose on both acromial processes.

The Gough's Cave 1 claviculae are compared to those of late Upper Paleolithic and Mesolithic (LUP/Meso) males and females in Tables 2 and 3.
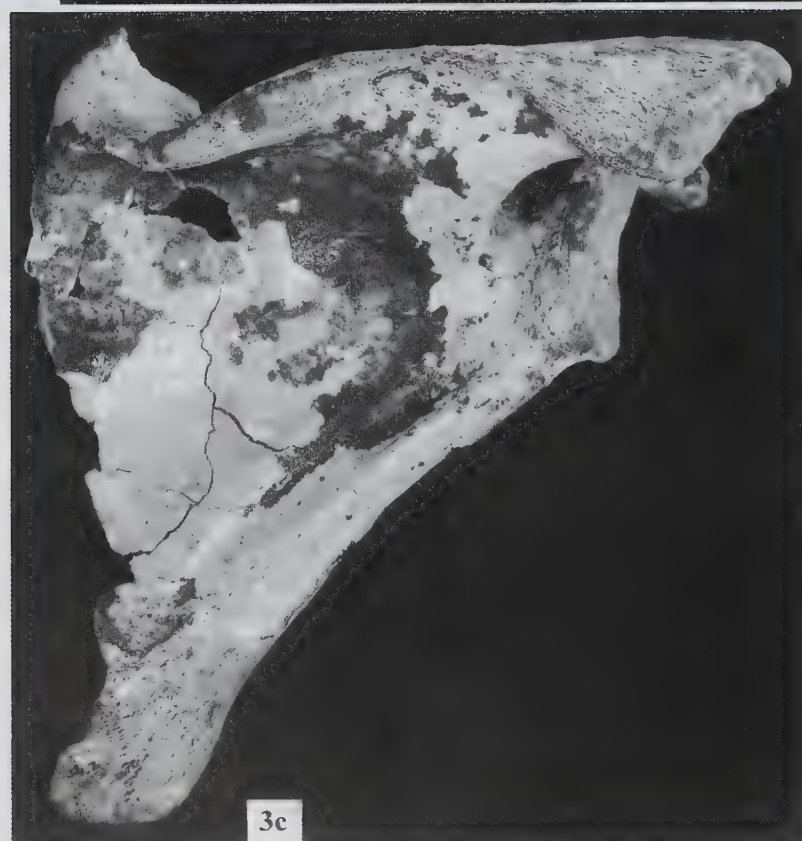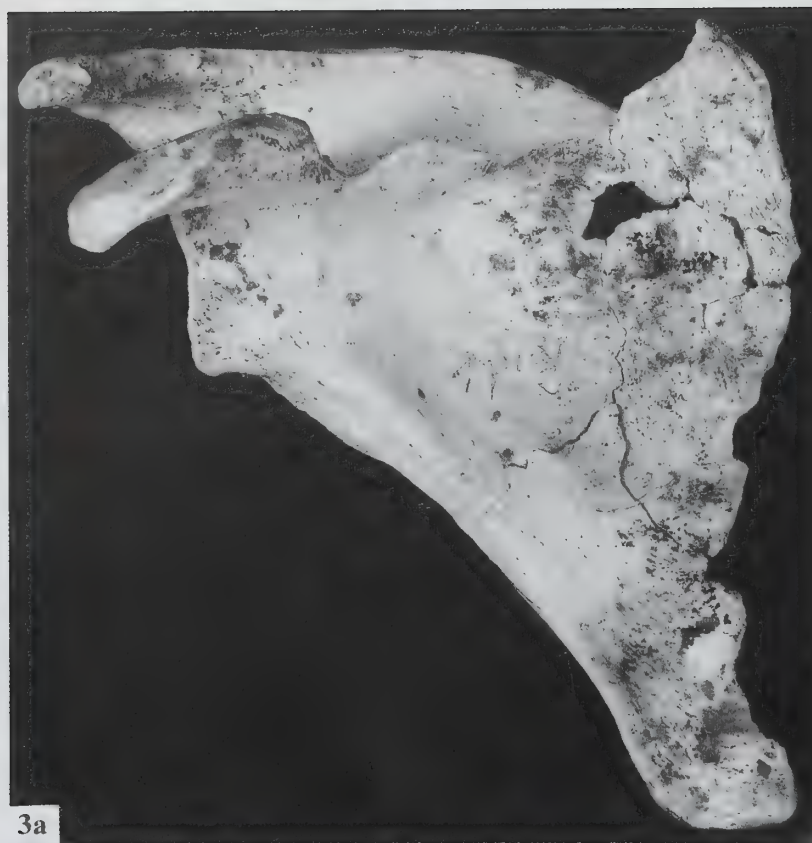
**Fig. 3** Gough's Cave 1 right scapula, in ventral (a), lateral (b), dorsal (c) and superior (d) views; × 0.8.

## SCAPULAR REMAINS

Only the right-side scapula is preserved (Fig. 3). The bone is largely complete, lacking only the superior angle (including some of the body on the *M. supraspinatus* surface) and vertebral border (and the adjacent 1-1.5cm of the body) from just distal of the root of the spine to the inferior angle. Scapular metrics are provided in Tables 4 and 5.

All of the observable secondary centres of ossification are fully fused and the epiphyseal lines are obliterated. These include the subcoracoid centre, the infraglenoid centre, the acromial centre, and the vertebral border centre (at least at the root of the spine – the only place this centre can be evaluated). It is possible that the vertebral border – inferior angle centre of ossification was not fully fused along its entire length, and that the preserved portion of the inferior angle represents an epiphyseal surface. Reconstructive materials obscure observation of the inferior angle, making evaluation of the state of fusion of the growth centre difficult.

The glenoid fossa is piriform (pear shaped) and has a very strong dorsal orientation. The dorsal margin of the articular surface rounds off onto the base along the dorsal edge, especially on the dorsoinferior margin. The articular surface of the glenoid fossa is irregular but there does not appear to be a central pit (McCown & Keith, 1939) (again, reconstructive materials obscure the articular morphology). The attachment for the glenoid labrum can be made out along the ventral margin of the articular surface, but disappears along the dorsal edge where the articular surface rounds off onto the base.

The infraglenoid tubercle begins as a very large attachment area on the dorsoinferior edge and dorsal part of the inferior edge of the glenoid. The tubercle is very large and elongated superoinferiorly (extending 32.6mm below the inferior margin of the glenoid fossa). The surface of the infraglenoid tubercle itself is finely rugose. The axillary crest (the attachment site for the fascia separating *M. subscapularis* and *M. teres minor*) is blunt and rounded, and runs along the dorsal portion of the axillary border for most of its length (Fig. 3b). At the distal end of the inferior *M. teres minor* attachment area the axillary crest veers dorsally and forms a rather strong crest on the dorsolateral edge of the axillary border. This morphology

**Table 4** Dimensions (mm) of the Gough's Cave 1 right scapula.

| | |
|---|---|
| Morphological length (M-2) | 100.0 |
| Infraspinatus breadth (M-5a) | 124.0 |
| Basal spinous length (M-8) | 79.4 |
| Spino-acromial length[a] | 130.0 |
| Spinal thickness[b] | 11.5 |
| Acromio-glenoid distance[c] | 45.4 |
| Axillary border length (M-3) | 126.6 |
| Functional axillary border length[d] | 139.0 |
| Mid-axillary border thickness[e] | 12.5 |
| Spino-glenoid angle (M-22) | 86° |
| Axillo-glenoid angle (M-17) | 35° |
| Axillo-spinal angle (M-16) | 60° |
| Glenoid maximum length (M-12) | 38.0 |
| Glenoid maximum breadth (M-13) | 26.1 |
| Glenoid articular length[f] | 34.7 |
| Glenoid articular breadth[f] | 24.8 |

Martin numbers (M=#: Martin, 1928) for measurements are provided where appropriate.
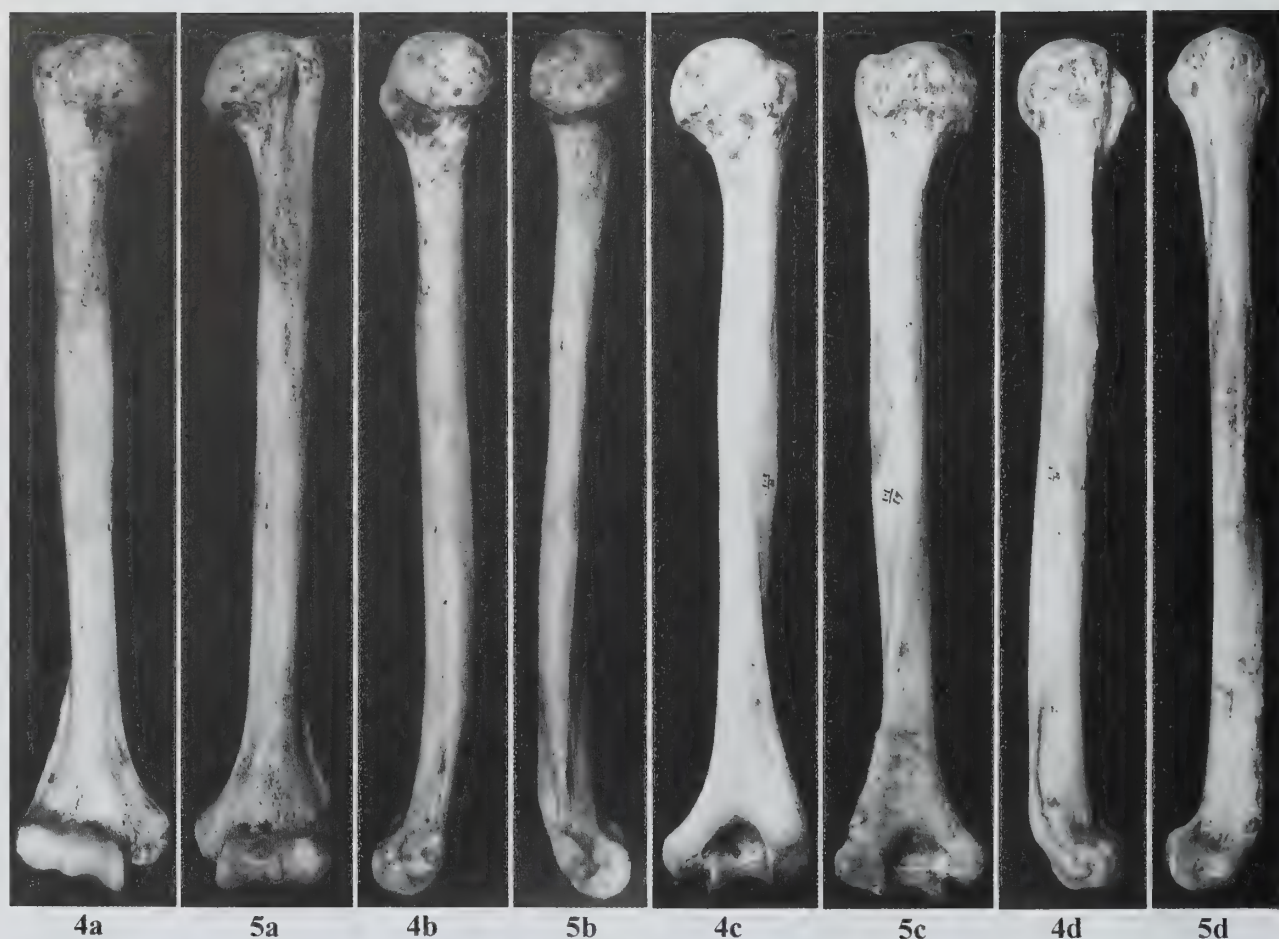[a] vertebral border at the spine to the tip of the acromion.
[b] maximum superoinferior thickness along the middle of the spine.
[c] center of glenoid fossa to the tip of the acromion.
[d] center of glenoid fossa to the most caudal point on the inferior angle.
[e] dorsoventral diameter of the mid-axillary border, including dorsal and ventral pillars as present.
[f] glenoid fossa length and breadth taken across the internal margins of the glenoid labrum attachment.

suggests that the *M. subscapularis* extended dorsally around the axillary border and had some fibres attached to the dorsal side of the lateral edge of the scapula at this level. The dorsal pillar (see Churchill, 1994) is laterally placed (running along the lateral-most edge of the axillary border) and well developed, and forms a deep sulcus on the body just medial of the pillar. The ventral pillar is medially positioned and is very strong, leaving a long, wide and shallow sulcus on the ventral aspect of the axillary border. Gough's Cave 1's scapular axillary border thus presents a ventral sulcus morphology similar to that seen in high frequencies in recent samples of European (and European-descent) populations (Trinkaus, 1977; Frayer, 1992; Churchill, 1996). On the dorsal aspect of the axillary border, there is what appears to be a vascular groove separating the infraglenoid tubercle and the superior portion of the attachment area for *M. teres minor*. This groove may indicate an accessory artery in the scapular anastomotic complex, one arising either from the root of the subscapular artery or perhaps stemming directly from the axillary artery. The groove for the circumflex scapular artery can be seen clearly dividing the *M. teres minor* origin further distally on the border. The *M. teres minor* attachment areas are poorly defined, the superior attachment area is not flattened and neither area is rugose. There is a small lateral flange for *M. teres major* and some flattening of the distal end of the axillary border.

There is little-to-no curvature of the body of the scapula. With the scapula held in anatomical position, the lateral edge of the acromion is broad dorsoventrally (measuring 49mm). The lateral edge of the acromion bears a rugose strip for the attachment of *M. deltoideus* along its entire length. The superior/dorsal surface of the spine is sinuous. The *M. trapezius* insertion area is not rugose. On the coracoid process, the lateral edge bears two small depressions with small crests for the *M. coracobrachialis* and *M. biceps brachii* short head attachments. The scapular notch is relatively broad.

## HUMERAL REMAINS

Both humeri are virtually complete (Figs 4, 5). The right-side has some damage to the dorsal surface of the head and this area is filled in with plaster. The left-side has some erosion to the medial surface of the head and what appears to be an erosional defect on the superoventral surface of the trochlea (see below). Otherwise, the two bones are very well preserved.

There is a very slight trace of an epiphyseal line on the anterior and medial surfaces of the proximal metaphysis just below the lesser tubercle and the articular surface of the head. The line is more apparent on the right humerus than on the left. On both humeri the line is largely obliterated on the dorsal and lateral surfaces. Even though the line is visible, the head is fully fused and the lines are near obliteration. Distally, the distal epiphyses and the medial epicondyle secondary centres of ossification are fully fused and the lines obliterated on both humeri.

The two sides are largely symmetrical with respect to size, robusticity and most details of morphology (Table 6). Although both humeri are similar in size and rugosity of muscle markings, the left-side seems to be the generally more muscle marked of the two. The humeri are not markedly robust. There is no notable curvature to the diaphyses in any plane. The deltoid tuberosities are neither large nor projecting, such that the diaphyses are of uniform dimension (save for a slight swelling at the deltoid tuberosity) along the shaft from every perspective. The head of the right humerus is dorsomedially directed (producing a torsion angle of 141°), while the left has a more medially oriented head (torsion angle = 166°).

**Figs 4, 5**   Gough's cave 1 humeri in ventral (a), medial (b), dorsal (c) and lateral (d) views; **4,** right-side humerus; **5,** left-side humerus; × 0.37.

**Table 5**   Comparative scapular dimensions (mean, SD, n)

|                           | Gough's Cave 1 (right) | LUP/Meso ♂ (right + left) | LUP/Meso ♀ (right + left) |
|---------------------------|:----------------------:|:-------------------------:|:-------------------------:|
| Morphological length      | 100.0                  | 139.4, 34.6, 4            | –                         |
| Axillary border length    | 126.6                  | 129.9, 5.6, 9             | 123.0, – , 2              |
| Glenoid articular length  | 34.7                   | 35.7 2.5, 8               | 32.1, 1.7, 7              |
| Glenoid articular breadth | 24.8                   | 26.6, 1.7, 6              | 23.1, 1.4, 7              |
| Glenoid index[a]          | 71.5                   | 73.7, 2.2, 6              | 72.1, 4.1, 7              |

All measurements are in millimeters and are defined in Table 4.
[a] Glenoid index = (articular breadth/articular length) x100.

The articular surfaces of the heads are fairly round, the left-side seems to be somewhat more oval shaped (with the long axis running superoinferiorly) than the right. The articular surfaces are smooth (save for erosional damage) and free of any signs of degeneration.

The right humerus has some erosion over the lateral surface of the greater tubercle, and the only muscle attachment area not eroded is the 'facet' for the insertion of *M. teres minor*. On the left-side the greater tubercle is well preserved, revealing a distinct 'facet' for *M. teres minor* and a more diffuse attachment area for *M. supraspinatus* and *M. infraspinatus*. The attachment area for these muscles is smooth and there is no clear separation between the facets for the two muscles. Both sides have pronounced intertubercular sulci formed medially by superoinferior running pillars extending from the lesser tuberosities along the insertion areas for *M. latissimus dorsi* and *M. teres major*, and laterally by pronounced crests for *M. pectoralis major*. The pillars are non-rugose (except at the muscle attachment areas) and the *M. pectoralis major* scars are only mildly rugose.

The deltoid tuberosities are not pronounced, but appear instead as slightly projecting, rugose crests. Indentations can be seen on both sides at the intersection of the proximal deltoid tuberosity with the inferior portion of the attachment of the pectoralis major muscle (the indentation is slightly more pronounced on the right-side). The indentation is best seen in medial or lateral view (Figs 4b, 4d, 5b, 5d). On the right-side there is a very slight musculoskeletal stress marker

**Table 6**  Dimensions (mm) of the Gough's Cave 1 humeri.

|  | Right | Left |
|---|---|---|
| Maximum length (M-1) | 322 | 322 |
| Articular length (M-2) | 316 | 318 |
| Midshaft maximum diameter (M-5) | 22.2 | 21.9 |
| Midshaft minimum diameter (M-6) | 17.0 | 15.2 |
| Midshaft circumference (M-7a) | 65 | 63 |
| Distal minimum circumference (M-7) | 62 | 61 |
| Head anteroposterior diameter (M-10) | (40.2) | 40.1 |
| Epicondylar breadth (M-4) | 58.0 | 57.5 |
| Distal articular breadth (M-12a) | 43.0 | 43.0 |
| Capitular breadth (M-12) | 21.0 | 19.0 |
| Trochlear breadth (M-11) | 20.2 | 21.1 |
| Trochlear max. anteroposterior diam.(M-13) | 24.9 | 23.9 |
| Medial epicondyle projection[a] | 18.3 | 16.7 |
| Lateral epicondyle projection[b] | 19.7 | 20.1 |
| Olecranon fossa breadth (M-14) | 23.8 | 23.9 |
| Olecranon fossa depth (M-15) | 12.2 | 12.2 |
| *M. pectoralis major* sulcus breadth[c] | 5.9 | 5.6 |
| Deltoid tuberosity width[d] | 11.5 | 13.3 |
| Deltoid tuberosity circumference[e] | 68 | 64 |
| Cubital angle (M-16) | 113° | 101° |
| Torsion angle (M-18) | 141° | 166° |

Martin numbers (M-#: Martin, 1928) for measurements are provided where appropriate.
[a] medial trochlear margin to the most projecting portion of the epicondyle.
[b] lateral trochlear margin to the most projecting tip of the epicondyle.
[c] maximum breadth (mediolateral) of the middle of the muscle insertion area.
[d] distance between the apices of the delimiting crests of the tuberosity taken at 5/12's of humeral maximum length, following Endo (1971).
[e] shaft circumference taken at 5/12's of humeral maximum length, following Endo (1971).

('enthesopathy': Dutour, 1986; Hawkey & Merbs, 1995) in the anterior crest of the deltoid just inferior of this depression. A similar but smaller projection can be seen at the same location on the left-side. The deltoid tuberosities are narrow in anterolateral view and are two-crested on both humeri. The posterior crest on the left humerus

is more rugose than the posterior crest on the right humerus (the right-side crest is very mildly rugose).

The other muscle attachment areas on the shaft are non-rugose (including *M. brachialis*, and the medial and lateral heads of *M. triceps brachii*). There is some slight rugosity along the *M. coraco-brachialis* insertions on both humeri.

Distally, the medial epicondyles are very large in superoinferior dimension but do not project very far mediolaterally, giving them a squat appearance. Both medial epicondyles present smooth but irregular surfaces where the common flexor tendon attaches. On the left-side there is a distinct crest on the anterosuperior edge of the attachment area, between the medial epicondyle proper and the shaft of the humerus. No such crest is apparent on the right-side. The lateral supracondylar ridges also seem well developed. The common extensor tendon origins are represented by small, smooth areas, and the *M. anconeus* origins are represented on both sides by smooth, thin semi-circular ridges that do not join the common extensor attachment areas.

The distal articular surfaces are relatively small, and have deep medial and lateral grooves. The lateral grooves (separating the lateral trochlear margin from the capitulum) are very wide and distinct. The capitullae are very small superoinferiorly and are slightly indented on their inferolateral surfaces, giving them a slightly laterally pointed appearance in anterior view. The left trochlea has an oval eroded patch (measuring 13mm mediolaterally by 9.5mm superoinferiorly) on its anterosuperior surface. This appears to be post-mortem in nature, and there is no corresponding defect on the left ulna, ruling out osteoarthritic eburnation. No other signs of degeneration are present on the distal articulations.

From the dorsal perspective, the distal medial pillars are relatively broad. The lateral pillars are also broad, and the surfaces behind the capitullae are flat and at angles of ca. 145° to the dorsal surfaces of the lateral pillars. The olecranon fossae are relatively small but deep.

Comparative data on other late Pleistocene/early Holocene human humeri are provided in Tables 7 and 8.

**Table 7**  Comparative humeral osteometrics (mean, SD, n).

|  | Gough's Cave 1 | LUP/Meso ♂ | LUP/Meso ♀ |
|---|---|---|---|
| *Right humeri* |  |  |  |
| Maximum length[a] | 322 | 307.3, 12.9, 17 | 287.0, 13.7, 9 |
| Midshaft maximum diameter | 22.2 | 23.9, 1.8, 17 | 20.7, 1.8, 10 |
| Midshaft minimum diameter | 17.0 | 17.7, 1.0, 17 | 15.4 1.6, 10 |
| Distal minimum circumference | 62 | 64.1, 4.1, 18 | 55.3, 5.2, 9 |
| Head anteroposterior diameter | (40.2) | 43.6, 2.8, 13 | 37.8, 3.2, 7 |
| Epicondylar breadth | 58.0 | 61.9, 2.2, 16 | 56.4, 2.9, 4 |
| Distal articular breadth | 43.0 | 42.8, 2.4, 16 | 39.2 4.3, 7 |
| Deltoid tuberosity width | 11.5 | 17.2, 2.8, 17 | 13.8, 2.2, 11 |
| Deltoid tuberosity circumference | 68 | 71.5, 3.9, 16 | 62.5, 4.4, 11 |
| *Left humeri* |  |  |  |
| Maximum length[a] | 322 | 313.4, 12.1, 12 | 287.4, 7.5, 10 |
| Midshaft maximum diameter | 21.9 | 23.4, 2.5, 13 | 20.2, 1.2, 9 |
| Midshaft minimum diameter | 15.2 | 17.0, 2.0, 14 | 15.8, 1.0, 9 |
| Distal minimum circumference | 61 | 62.7, 5.7, 12 | 55.9, 2.6, 8 |
| Head anteroposterior diameter | 40.1 | 43.1, 1.6, 14 | 39.2, 1.5, 5 |
| Epicondylar breadth | 57.5 | 61.1, 3.1, 11 | 54.7, 1.8, 7 |
| Distal articular breadth | 43.0 | 43.2, 2.1, 10 | 38.5, 2.5, 7 |
| Deltoid tuberosity width | 13.3 | 16.9, 3.4, 13 | 13.6, 2.3, 10 |
| Deltoid tuberosity circumference | 64 | 69.5, 6.7, 13 | 59.7, 3.8, 10 |

All measurements are in millimeters and are defined in Table 6.
[a] includes estimated lengths for some comparative specimens

**Table 8**  Mid-shaft humeral cross-sectional properties, standardized[a] (mean, SD).

|  | Gough's Cave 1 | LUP/Meso ♂ (n=17) | LUP/Meso ♀ (n=10) |
|---|---|---|---|
| *Right humeri* |  |  |  |
| Total area (TA) | 307.3 | 363.2, 59.4 | 314.7, 36.0 |
| Cortical area (CA) | 221.1 | 260.8, 52.1 | 224.4, 43.2 |
| Medullary area (MA) | 86.2 | 102.4, 32.5 | 90.2, 26.2 |
| ML 2nd moment of area ($I_x$) | 682.6 | 955.0, 296.5 | 789.7, 192.7 |
| AP 2nd moment of area ($I_y$) | 783.9 | 1104.0, 404.6 | 750.1, 207.5 |
| Maximum 2nd moment of area ($I_{max}$) | 952.4 | 1241.1, 487.1 | 1048.9, 292.4 |
| Minimum 2nd moment of area ($I_{min}$) | 514.1 | 718.5, 232.8 | 531.2, 153.7 |
| Polar moment of area (J) | 1466.5 | 2059.1, 684.7 | 1539.8, 384.5 |
| Percent cortical area (%CA) | 71.9 | 71.7, 8.0 | 70.2, 8.3 |
| $I_x/I_y$ | 0.871 | 0.893, 0.132 | 1.079, 0.168 |
| $I_{max}/I_{min}$ | 1.853 | 1.712, 0.313 | 1.901, 0.426 |
| *Left humeri* |  | (n=12) | (n=9) |
| Total area (TA) | 271.1 | 350.3, 59.9 | 297.7, 32.0 |
| Cortical area (CA) | 180.2 | 253.4, 53.6 | 207.0, 32.6 |
| Medullary area (MA) | 90.9 | 96.8, 29.3 | 90.7, 33.9 |
| ML 2nd moment of area ($I_x$) | 452.3 | 832.2, 251.9 | 659.2, 145.2 |
| DV 2nd moment of area ($I_y$) | 649.0 | 1106.7, 423.3 | 662.0, 152.4 |
| Maximum 2nd moment of area ($I_{max}$) | 723.9 | 1313.3, 412.9 | 811.6, 187.8 |
| Minimum 2nd moment of area ($I_{min}$) | 377.4 | 730.0, 246.7 | 473.5, 91.8 |
| Polar moment of area (J) | 1101.3 | 1938.8, 659.3 | 1321.2, 275.9 |
| Percent cortical area (%CA) | 66.5 | 72.2, 7.3 | 71.2, 10.7 |
| $I_x/I_y$ | 0.697 | 0.803, 0.201 | 1.006, 0.184 |
| $I_{max}/I_{min}$ | 1.918 | 1.837, 0.318 | 1.695, 0.136 |

See text for definition of measurements.

[a] Cross-sectional strength measures standardized to humeral articular length (HAL). Areal measures (TA, CA and MA) were divided by $HAL^2$ and multiplied by $10^5$. 2nd moments of area ($I_x$, $I_y$, $I_{min}$, $I_{max}$, J) were divided by $HAL^4$ and multiplied by $10^9$.

**Table 9**  Dimensions (mm) of the Gough's Cave 1 ulnae.

| Measurement | Right | Left |
|---|---|---|
| Maximum length (M-1) | – | (270) |
| Articular length (M-2) | – | 250 |
| Olecranon length (M-8) | 14.8 | – |
| Olecranon height (M-7) | 27.7 | – |
| Olecranon breadth (M-6) | 24.0 | – |
| Trochlear notch chord (M-7(1)) | 23.5 | – |
| Coronoid height[a] | 36.3 | 34.9 |
| Radial facet maximum diameter[b] | 19.9 | 18.3 |
| Radial facet minimum diameter[b] | 10.9 | 10.6 |
| Coronal trochlear angle (M-15) | 14° | – |
| Diaphyseal sagittal trochlear angle (M-15a) | 21° | – |
| Proximal anteroposterior diameter[c] | 18.3 | 18.4 |
| Proximal transverse diameter[c] | 18.8 | 18.7 |
| Proximal circumference[c] | 51 | 49 |
| Crest anteroposterior diameter (M-11) | 15.3 | 13.7 |
| Crest mediolateral diameter (M-12) | 14.3 | 15.0 |
| Midshaft anteroposterior diameter | 12.2 | 12.2 |
| Midshaft mediolateral diameter | – | 13.2 |
| Midshaft circumference | – | 42 |
| Distal minimum circumference (M-3) | 37 | – |
| Pronator quadratus crest maximum diameter[d] | 12.8 | – |
| Pronator quadratus crest minimum diameter[d] | 10.6 | – |
| Pronator quadratus circumference[d] | 38 | – |
| Head breadth[e] | 16.9 | 17.0 |

Martin numbers (M-#: Martin, 1928) for measurements are provided where appropriate.

[a] maximum anteroposterior diameter from the dorsal surface of the bone to the anterior tip of the coronoid process (McHenry *et al.*, 1976).

[b] maximum and minimum diameters of the articular facet for the radial head.

[c] taken at the level of the distal border of the ulnar tuberosity (McHenry *et al.*, 1976).

[d] shaft maximum and minimum diameters and circumference at the most projecting portion of the pronator quadratus crest.

[e] mediolateral diameter of the ulnar head.

## ULNAR REMAINS

Both ulnae are largely complete (Figs 6, 7, Table 9). The right-side is somewhat better preserved than the left, but is missing a 4cm portion of the diaphysis from about midshaft distally. This area has been reconstructed in plaster. With the exception of the missing diaphyseal fragment, the bone is complete. The left-side is missing the anterior half of the olecranon process (from the anterior edge of the *M. triceps brachii* insertion), including some of the olecranon articular surface in the trochlear notch. There is also some damage to the surface of the left-side distal shaft in the region of the *M. pronator quadratus* crest. Otherwise, the bone is very well preserved.

The proximal and distal epiphyses are fully fused. The left-side ulna has a closed but still (barely) visible epiphyseal line between the head and shaft. All of the other epiphyseal lines are fully obliterated.

Both ulnae are of moderate robusticity (Tables 10 and 11). The right-side shaft has a lateral curve to the distal end (as seen in volar view), beginning in the area around the *M. pronator quadratus* crest. The left-side diaphysis is straight, but has had some damage to and refitting of the distal end, perhaps affecting the appearance of distal shaft. The shafts are also straight in lateral view.

The trochlear notch on the right-side (the left is damaged) opens anteroproximally (Fig. 8). Neither side has a very marked separation (as either a crest or sulcus) between the coronoid and olecranon articular surfaces in the notch, nor does either side express a sagittally oriented crest in the notch. There is no evidence of degenerative changes to the trochlear or radial notches of either side. The radial notches are relatively large, and are oriented superolaterally.

The *M. triceps brachii* insertion on the olecranon process is mildly rugose (on the right ulna, this region can't be fully evaluated in the left), with vertical striations on the posterior edge of the olecranon but no spurring or indications of musculoskeletal stress lesions. The

**6a**   **7a**   **6b**   **7b**   **6c**   **7c**   **6d**   **7d**

**Figs 6, 7**   Gough's Cave 1 ulnae, in ventral (a), medial (b), dorsal (c) and lateral (d) views; **6**, right-side ulna; **7**, left-side ulna; × 0.5.
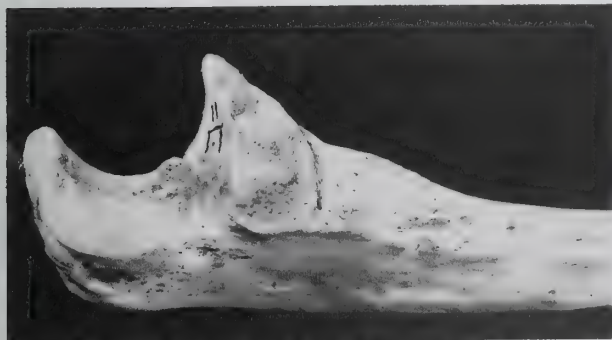


**Fig. 8**   Gough's Cave 1 right ulna in lateral view; × 1.

*M. anconeus* insertion area is mildly rugose, occupying a narrow ridge (between the medial and lateral surfaces of the proximal shaft) on the dorsal surface of the shaft. This mildly rugose line continues distally until it joins with the line marking the aponeurotic attachment of *M. flexor digitorum profundus*, *M. flexor carpi ulnaris* and

*M. extensor carpi ulnaris*. Supinator crests of both sides are well developed, beginning as pronounced crests arising from the inferodistal margins of the radial notches (Fig. 8). The crests continue distally to a half centimeter or so below the *M. brachialis* scar, where they stop and then resume again another 10–20mm distally. The distal portions of the *M. supinator* ridges follow the interosseous crests (lying just posterior to and on the lateral surface of the interosseous crests), about one-third of the way down the shaft. The posterior edge of the proximal portion of the *M. supinator* attachment area is also marked by a crest on the lateral surface below the trochlea. The *M. brachialis* scars are moderately rugose, and present themselves as small raised patches (roughly 13mm proximodistally × 9mm mediolaterally on both sides). The area between the scars and the coronoid processes is mildly rugose. No markings are evident on either side for *M. pronator teres*. There is a large tubercle present on the anteromedial corner of the coronoid process in the area of the origin of the ulnar head of *M. flexor digitorum superficialis* on the right-side. This area is somewhat damaged in the left-side ulna, but it is certain that the tubercle, if indeed it existed, was not nearly as large as that of the right.

**Table 10**  Comparative ulnar osteometrics (mean, SD, n).

|  | Gough's Cave 1 | LUP/Meso ♂ | LUP/Meso ♀ |
|---|---|---|---|
| *Right ulnae* | | | |
| Olecranon length | 14.8 | 17.1, 2.6, 15 | 16.7, 2.0, 4 |
| Olecranon height | 27.7 | 27.1, 1.9, 13 | 23.8, 1.4, 4 |
| Olecranon breadth | 24.0 | 25.7, 1.3, 12 | 23.6, 1.1, 4 |
| Trochlear notch chord | 23.5 | 27.0, 3.6, 10 | 22.7, 2.7, 3 |
| Coronoid height | 36.3 | 37.4, 1.6, 12 | 32.2, 2.1, 6 |
| Radial facet maximum diam | 19.9 | 16.8, 1.8, 9 | 16.4, –, 2 |
| Radial facet minimum diam | 10.9 | 11.6, 0.6, 9 | 11.2, –, 2 |
| Proximal AP diameter | 18.3 | 15.7, 1.6, 13 | 15.2, 2.0, 5 |
| Proximal transverse diam | 18.8 | 16.8, 2.0, 13 | 13.7, 1.7, 5 |
| Proximal circumference | 51 | 50.5, 3.8, 12 | 45.0, 2.6, 5 |
| Midshaft AP diameter | 12.2 | 14.6, 1.9, 5 | 12.8, –, 1 |
| Pron. quadratus max diam | 12.8 | 13.6, 1.4, 11 | 12.1, 1.2, 4 |
| Pron. quadratus min diam | 10.6 | 10.3, 0.9, 11 | 9.6, 0.9, 4 |
| Pron. quadratus circum | 38 | 38.9, 3.1, 11 | 35.3, 2.9, 4 |
| *Left ulnae* | | UP/Meso ♂ | UP/Meso ♀ |
| Maximum length[a] | (270) | 263.9, 10.6, 14 | 245.8, 8.3, 4 |
| Articular length[a] | 250 | 241.6, 10.6, 15 | 224.7, 7.4, 7 |
| Coronoid height | 34.9 | 36.7, 1.1, 12 | 33.3, 1.0, 4 |
| Radial facet maximum diam | 18.3 | 16.8, 1.3, 9 | 16.4, 1.6, 3 |
| Radial facet minimum diam | 10.6 | 11.1, 1.2, 9 | 10.1, 0.4, 4 |
| Proximal AP diameter | 18.4 | 15.5, 2.2, 11 | 15.4, 1.6, 8 |
| Proximal transverse diam | 18.7 | 15.3, 2.8, 11 | 13.4, 1.7, 8 |
| Proximal circumference | 49 | 48.0, 6.3, 11 | 44.2, 3.5, 7 |
| Midshaft AP diameter | 12.2 | 15.2, 1.2.3 | 13.5, 0.6, 4 |
| Midshaft ML diameter | 13.2 | 14.5, 1.5, 3 | 11.7, 0.5, 4 |

All measurements are in millimeters and are defined in Table 9.

[a] includes estimated lengths for some comparative specimens.

**Table 11**  Mid-proximal ulnar cross-sectional properties, standardized[a] (mean, SD).

|  | Gough's Cave 1 | LUP/Meso ♂ (n=4) | LUP/Meso ♀ (n=2) |
|---|---|---|---|
| *Right ulnae* | | | |
| Total area (TA) | 228.8 | 266.8, 36.7 | 192.0 |
| Cortical area (CA) | 210.1 | 222.7, 33.3 | 177.1 |
| Medullary area (MA) | 18.7 | 44.1, 14.7 | 14.9 |
| ML 2nd moment of area ($I_x$) | 417.9 | 534.8, 235.8 | 352.3 |
| AP 2nd moment of area ($I_y$) | 491.5 | 655.3, 143.7 | 278.3 |
| Maximum 2nd moment of area ($I_{max}$) | 536.8 | 714.5, 184.3 | 360.9 |
| Minimum 2nd moment of area ($I_{min}$) | 372.7 | 475.6, 150.0 | 269.8 |
| Polar moment of area (J) | 909.5 | 1190.1, 325.7 | 630.7 |
| Percent cortical area (%CA) | 91.8 | 83.5, 5.5 | 92.5 |
| $I_x/I_y$ | 0.850 | 0.814, 0.306 | 1.269 |
| $I_{max}/I_{min}$ | 1.440 | 1.528, 0.203 | 1.338 |
| *Left ulnae* | | (n=3) | (n=3) |
| Total area (TA) | 221.8 | 277.7, 17.2 | 244.0, 19.3 |
| Cortical area (CA) | 195.7 | 242.9, 27.4 | 221.6, 23.5 |
| Medullary area (MA) | 26.1 | 34.8, 24.5 | 22.5, 12.6 |
| ML 2nd moment of area ($I_x$) | 335.7 | 632.9, 187.8 | 562.9, 86.1 |
| DV 2nd moment of area ($I_y$) | 487.3 | 676.1, 141.1 | 443.4, 120.3 |
| Maximum 2nd moment of area ($I_{max}$) | 488.9 | 784.4, 129.1 | 610.4, 110.3 |
| Minimum 2nd moment of area ($I_{min}$) | 334.2 | 524.6, 79.4 | 395.9, 52.6 |
| Polar moment of area (J) | 823.1 | 1309.1, 179.3 | 1006.3, 160.4 |
| Percent cortical area (%CA) | 88.2 | 87.5, 8.7 | 90.8, 5.0 |
| $I_x/I_y$ | 0.689 | 0.975, 0.376 | 1.319, 0.331 |
| $I_{max}/I_{min}$ | 1.463 | 1.507, 0.267 | 1.537, 0.124 |

See text for definition of measurements.

[a] Cross-sectional strength measures standardized to ulnar articular length (UAL). Areal measures (TA, CA and MA) were divided by $UAL^2$ and multiplied by $10^5$. 2nd moments of area ($I_x$, $I_y$, $I_{min}$, $I_{max}$, J) were divided by $UAL^4$ and multiplied by $10^9$.

On both sides, the distal end of the interosseous crest branches into two crests – more strongly so on the right-side but also to some extent on the left. This may reflect a division of the membranes for *M. flexor digitorum profundus* anteriorly and *M. extensor indicis* posteriorly. The right-side *M. pronator quadratus* crest (this area is damaged in the left ulna) is relatively small but is clearly discernable as a narrow, projecting crest.

The styloid processes are relatively long. There are no signs of any degenerative changes to the distal articular surfaces on either side.

**Table 12** Dimensions (mm) of the Gough's Cave 1 radii.

| Measurement | Right | Left |
|---|---|---|
| Maximum length (M-1) | – | 248 |
| Articular length (M-2) | – | 235 |
| Proximal anteroposterior diameter[a] | 13.5 | 13.1 |
| Proximal mediolateral diameter[a] | 12.2 | 12.8 |
| Proximal circumference[a] | 41 | 41 |
| Crest anteroposterior diameter (M-5) | 12.4 | 11.7 |
| Crest mediolateral diameter (M-4) | 17.1 | 15.6 |
| Midshaft anteroposterior diameter (M-5a)[b] | 12.0 | 11.9 |
| Midshaft mediolateral diameter (M-4a)[b] | 16.9 | 15.1 |
| Midshaft circumference (M-5(5))[b] | 46 | 42 |
| Distal minimum circumference (M-3) | 41 | (41) |
| Head-neck length (M-1a) | 33.0 | 31.3 |
| Neck-shaft angle (M-7) | 6° | 6° |
| Head anteroposterior diameter (M-5(1)) | 21.1 | 22.4 |
| Head mediolateral diameter (M-4(1)) | 21.2 | 21.3 |
| Head circumference (M-5(3)) | 69 | 71 |
| Neck anteroposterior diameter (M-5(2)) | 14.7 | 15.1 |
| Neck mediolateral diameter (M-4(2)) | 12.4 | 14.7 |
| Neck circumference (M-5(4)) | 44 | 46 |
| Bicipital tuberosity length[c] | 22.4 | 21.5 |
| Bicipital tuberosity breadth[d] | 14.1 | 14.2 |
| Distal breadth (M-5(6)) | – | 27.7 |
| Distal depth[e] | – | 15.4 |
| Carpal articular breadth[f] | – | 27.3 |

Martin numbers (M-#: Martin, 1928) for measurements are provided where appropriate.
[a] taken midway between the bicipital tuberosity and the proximal end of the interosseous crest.
[b] right-side midshaft position was estimated using the more complete left-side radius.
[c] maximum proximodistal diameter of the tuberosity.
[d] maximum dorsovolar diameter of the tuberosity.
[e] maximum dorsovolar diameter of the distal epiphysis, not including the dorsal (Lister's) tubercle.
[f] maximum mediolateral diameter of the articular surface.

# RADIAL REMAINS

Both radii are preserved (Figs 9, 10). The right radius is missing the distal end from the region of the distal interosseous crest. The diaphysis has also been broken and refitted near midshaft. The left-side is more complete but has some damage to its distal end. The anterior surface of the left distal shaft, from slightly below midshaft to the epiphyseal end, is eroded and damaged, and the anterior surface of the distal metaphyseal area is missing. The proximal halves of both radii are in a good state of preservation.

The proximal (right and left) and distal (left) epiphyses are fully fused and the epiphyseal lines are obliterated. No degenerative changes are evident in any of the preserved articular surfaces.

The heads of both radii are slightly (but only slightly) oblong, with the long axis running anteromedial to posterolateral. The neck of the right radius is narrower in both anterior and lateral views compared to the left (Table 12). The radial tuberosity and anterior oblique crest also have a slightly greater development on the left-side. The radial tuberosities are proximodistally short (Table 12), moderately wide, but projecting medially (the left more so than the right). The anterior oblique crests extend about 3 cm below the radial tuberosities, and are well developed. The *M. supinator* insertion areas are smooth.

The proximal end of the left radius is generally larger and more robust than the right (in the head, neck and radial tuberosity dimensions: Table 12), but the right clearly has a greater development of the interosseous crest and shaft.

The shafts are relatively straight (in both anterior and lateral views) and are of moderate robusticity (Table 13). The *M. pronator teres* insertions are clearly defined and of moderate rugosity. The attachment sites for *M. pronator quadratus* and *M. brachioradialis* are too damaged on the left-side (and absent on the right) to say anything about. On the dorsal aspect of the distal left shaft, the dorsal ('Lister's') tubercle is very well developed.

**Table 13** Comparative radial osteometrics (mean, SD, n).

| | Gough's Cave 1 | LUP/Meso ♂ | LUP/Meso ♀ |
|---|---|---|---|
| *Right radii* | | | |
| Midshaft AP diam | 12.0 | 12.3, 0.4, 4 | 10.1, 0.9, 3 |
| Midshaft ML diam | 16.9 | 16.0, 1.4, 4 | 13.3, 1.8, 3 |
| Head-neck length | 33.0 | 31.8, 2.6, 12 | 31.9, 1.7, 5 |
| Neck-shaft angle | 6° | 8.8°, 3.4,12 | 11.1°, 5.1, 6 |
| Head AP diam | 21.1 | 22.7, 1.4, 8 | 20.8, 1.7, 3 |
| Head ML diam | 21.2 | 21.8, 1.4, 10 | 20.6, 1.8, 3 |
| Neck AP diam | 14.7 | 23.2, 1.2, 10 | 11.9, 1.4, 6 |
| Neck ML diam | 12.4 | 13.3, 1.3, 9 | 11.3, 1.0, 6 |
| Bicip. Tuberosity length | 22.4 | 21.8, 2.6, 12 | 22.0, 2.6, 7 |
| Bicip. Tuberosity breadth | 14.1 | 14.5, 1.2, 12 | 12.4, 1.3, 7 |
| *Left radii* | | UP/Meso ♂ | UP/Meso ♀ |
| Maximum length[a] | 248 | 243.9, 7.4, 10 | 226.8, 8.8, 4 |
| Articular length[a] | 235 | 228.5, 9.3, 13 | 215.2, 7.9, 5 |
| Midshaft AP diam | 11.9 | 11.9, 0.7, 4 | 10.0, 0.7, 3 |
| Midshaft ML diam | 15.1 | 14.9, 1.5, 4 | 12.5, 1.0, 3 |
| Head-neck length | 31.3 | 31.8, 1.7, 11 | 31.0, 3.3, 4 |
| Neck-shaft angle | 6° | 9.0°, 4.1, 10 | 12.8°, 7.0, 5 |
| Head AP diam | 22.4 | 22.9, 1.0, 12 | 17.7, 4.0, 3 |
| Head ML diam | 21.3 | 21.7, 0.6, 8 | 18.9, 2.3, 4 |
| Neck AP diam | 15.1 | 14.0, 1.0, 12 | 12.4, 0.9, 6 |
| Neck ML diam | 14.7 | 12.3, 3.9, 14 | 11.4, 1.0, 6 |
| Bicip. tubersoity length | 21.5 | 22.2, 2.5, 13 | 19.4, 1.8, 6 |
| Bicip. tuberosity breadth | 14.2 | 14.0, 1.7, 14 | 12.7, 1.0, 7 |

All measurements are in millimeters and are defined in Table 12.
[a] includes estimated lengths for some comparative specimens.

**Figs 9, 10**   Gough's Cave 1 radii, in ventral (a), medial (b), dorsal (c) and lateral (d) views; **9,** right-side radius (note that the distal end is reconstructed); **10,** left-side radius; × 0.5.

## COMPARATIVE MORPHOLOGY OF THE UPPER LIMB REMAINS

In most measures, the Gough's Cave 1 upper limb skeleton is comparable to that of other European males alive during the final Pleistocene and early Holocene. In both gross external and cross-sectional dimensions of the humerus, radius and ulna, Gough's Cave 1 is unremarkable compared to his contemporaries. These bones tend to be slightly longer (on average) than those of his male contemporaries, yet to have epiphyseal dimensions and diaphyseal diameters roughly equivalent to the mean values observed in the comparative sample males (Tables 7, 10 and 13). Thus relative to length, the upper limb long bones of Gough's Cave 1 are somewhat gracile when seen in the context of other similarly aged fossils. This characterization holds for size-standardized measures of the mechanical strength of the humerus and ulna as well (Tables 8 and 11), suggesting that the habitual biomechanical loads incurred in the upper limbs of Gough's Cave 1 were somewhat meager relative to other Upper Paleolithic and Mesolithic foragers.

Perhaps the most remarkable feature in the upper limbs (used here in the broad sense to include the pectoral girdles) is the robusticity of Gough's Cave 1's right clavicle. In terms of length, the right clavicle falls between the mean values for males and females in the comparative sample (Table 2). However, in external dimensions (Table 2) and unstandardized cross-sectional properties (Table 3), Gough's Cave 1's right clavicle tends to fall on or above the male sample means. The superoinferior, dorsoventral and maximum 2nd moments of area, as well as the polar moment of area, are two or more standard deviations above the (admittedly small) male sample means (Table 3). Given that Gough's Cave 1's claviculae were relatively short, the clavicular strength values are all the more striking. Consideration of the cross-sectional geometric properties presented in Table 3 shows that the large values for bending rigidity (2nd and polar moments of area) in Gough's Cave 1's right clavicle are due in part to the overall size of the cross-sections (TA). The right clavicle has a midshaft cortical area (CA) close to the comparative male mean, but this cortical bone is distributed further from the geometric centre of the section. This results in a relatively large medullary cavity, a relatively low percent cortical area, and relatively high 2nd moments of area.

A similar consideration of Gough's Cave 1's left clavicle shows it to be relatively gracile, at least in cross-sectional measures of strength (Table 3) if not in external dimensions (Table 2). Bilateral asymmetry in upper limb strength measures is certainly to be expected (see Churchill, 1994), and the degree of asymmetry seen here is not likely to be outside the range observed in fossil and recent, moderately to highly active foragers. What is curious about Gough's Cave 1 is the robusticity of the right clavicle in the context of an otherwise relatively gracile upper limb skeleton.

Gough's Cave 1's right clavicle has an $I_x/I_y$ ratio that is above but within one standard deviation of the male comparative sample mean (yet below the mean of females: Table 3), yet has an $I_{max}/I_{min}$ ratio considerably higher than the mean of the comparative samples. The angle formed between the plane of greatest bending rigidity and the dorsoventral plane passing through the centre of the section is 130° in the Gough's Cave 1 right clavicle, indicating an adaptation to bending in the superodorsal to inferoventral direction (*i.e.*, about an inferodorsal to superoventral axis). This might suggest an habitual generation of dorsoventrally oriented forces operating on the clavicle during full abduction of the humerus (in which scapular rotation on the thorax necessitates conjunct posterior axial rotation of the clavicle, bringing the superodorsal-inferoventral axis of the bone into the transverse plane of the body). While it is the case that the muscle scars for *M. deltoideus*, the major abductor of the humerus, are rugose on the clavicle (at least on the left side, this region is damaged in the right), scapulae and humeri, it is also the case that the humeral deltoid tuberosities are weakly developed. This, combined with the overall gracility of the other upper limb bones, makes it difficult to imagine a behavior pattern that could differentially load the clavicle more than the other bones of the limb. The asymmetry evident in the claviculae is also not apparent in the other upper limb remains (and in fact the reverse pattern is seen in the radii, with the left being slightly more robust than the right).

Actions involving forceful right-side scapular abduction (as in pushing on a heavy object with the arms abducted and flexed, that is, out in front of the body) or adduction (as in forcefully pulling something using motion at the shoulder) would be expected to generate bending moments in the transverse plane of the clavicle. However, such movements would also be expected to create bending stresses in the arm and forearm. Thus if Gough's Cave 1 were routinely engaged in an activity requiring forceful pulling or pushing with one limb (perhaps involving woodworking in the manufacture of tools, or perhaps trap setting), we would expect a marked degree of right-left asymmetry in bone strength and muscle scarring in the upper limbs overall. Occupationally induced habitual heavy loading of the bones and joints of the upper limb is known to promote clavicular robusticity. For example, Lane (1887) reported marked robusticity in the *lateral half* of the clavicle in milkmen that routinely carried heavy milk pails with their arms by their sides. While observations like this support the possibility that the robusticity of the Gouch's Cave 1 right clavicle reflects habitual labor induced ('occupational') loads, the nature of the robusticty (both in terms of bone shape and the observed asymmetry) and the lack of associated degenerative changes to the clavicular joints does not fit with known patterns of occupational changes to upper limb morphology (reviewed in Kennedy, 1989). Thus the behavior patterns that produced this morphology in Cheddar Man remain, for the time being, unknown.

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# Systematic affinity of *Acroporella assurbanipali* Elliott (Dasycladaceae), with notes on the genus *Neomeris*

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**SYNOPSIS.**    The holotype of the extinct Dasycladacean alga *Acroporella assurbanipali* Elliott is re-described and a reconstruction is presented. The status of the species is reviewed, and it is assigned to the genus *Neomeris*, subgenus *Larvaria*.

## INTRODUCTION

This paper deals with the systematic affinity of the Lower Cretaceous alga *Acroporella assurbanipali*, which is known only from the type-locality at Erbil Liwa, Iran. We present a new description based on a reinterpretation of the holotype, which is deposited in the Natural History Musem, London (Elliott collection). *A. assurbanipali* is reassigned to the genus *Neomeris*, subgenus *Larvaria*. The taxonomic status of *Acroporella* and *Neomeris* is also discussed.

## *ACROPORELLA ASSURBANIPALI* AND ITS RELATIONSHIP WITH THE GENUS *ACROPORELLA* (PRATURLON) EMEND. PRATURLON & RADOICIC

The genus *Acroporella* was established by Praturlon in 1964 and based on algal specimens from Upper Jurassic – Lower Cretaceous shelf limestones of the Central Apennines (Marsica, Central Italy). In that paper, Praturlon characterized the genus as simple thallus, with euspondyle and acrophorous primary laterals (= branches), and probably endosporous. The type species *Acroporella radoicici* has the following characters: cylindrical, not segmented dasycladaceae; branches acrophorous, simple, oblique to axis (15–45° on the horizontal), arranged in euspondyle alternating whorls; calcification reaching the axial cell; dimensions in mm (between brackets the extreme value): D=0.55 (0.36–0.70); d=0.25 (0.17–0.33); p=0.06 (0.05–0.07); w=8–12; h=0.1 (0.085–0.11); maximum measured length of the fragments=5.4; reproductive organs unknown.

Praturlon & Radoicic (1974), following the rules of the International Code of Botanical Nomenclature, changed the epithet from *A. raidoicici* to *A. radoicicae*. Moreover, on the basis of better preserved Barremian-Aptian material from Dinarides, they showed that the species bears four short secondary laterals per primary lateral set distally. Accordingly they proposed an emendation of the genus and gave the following diagnosis for *Acroporella*: 'Cylindrical, not segmented dasycladaceae, having whorls of primary branches distally ramified in clusters of button-like secondary twigs'.

However six years before the emendation by Praturlon & Radoicic (1974), Elliott had established the species *A. assurbanipali* from the Lower Cretaceus of Erbil Liwa, Iran. According to Elliott (1968) the species is characterised by: 'Cylindrical tubular calcified dasyclad, external diameter 1.36 mm, internal diameter 0.55 mm (40% of external); successive near-horizontal verticils, probably 3 or 4 per

mm of tube-length, of perhaps twelve radial branches each. The single branches communicate with the stem cavity by a pore of about 0.052 mm diameter: they then swell out to a fig- or flask-shaped cavity of 0.182 mm maximum diameter, narrow to a slightly curved tube of 0.078 mm diameter, and then at the outer surface flare out to a shallow terminal diameter of 0.156 mm'.

Since its proposal, *A. assurbanipali* has been overlooked by most authors. Granier & Deloffre (1993) re-assessed its taxonomic position and confirmed the affinity with *Acroporella*, but with reservations. One of the authors of the present paper (F. Barattolo) recently examined the Elliott collection at the Natural History Museum, London. Re-examination of the single specimen in thin section (holotype) and Elliott's description, allows us to propose a new interpretation of the anatomy of the alga. Accordingly, we assign the species to the genus *Neomeris*.

## *NEOMERIS* (LAMOUROUX, 1816), ITS SUBGENERA AND ALLIED GENERA

The genus was defined on an extant species from Jamaica (*Neomeris dumetosa* Lamouroux).

The alga is characterised by a cylindrical thallus bearing whorls of primary laterals. Each primary lateral bears at its outer end a single ovoid ampulla together with two secondary laterals. The laterals, usually those of secondary order, may produce a cortical layer (Valet, 1968; Berger & Kaever, 1992).

Seven species are known to live in tropical and subtropical seas where they populate protected microenvironments of the reef platform (Valet, 1979), in moderately exposed environments (e.g. *Neomeris mucosa*) and in tidal pools (e.g. *Neomeris cokeri*) (Taylor, 1972). According to Konishi & Epis (1962) a depth of 0–10 m and a temperature of 15–20°C are their optimal environmental conditions.

The main diagnostic characters utilised in botanical description of specific rank in extant *Neomeris* are: shape of primary laterals; shape of secondary laterals and their distal ends making a cortex or not; shape of fertile ampulla and cyst; shape of the plug set at the connection between primary laterals and ampulla; calcification (Génot, 1980).

In spite of its modest role in the modern marine environment, the genus *Neomeris* is well represented in the fossil record, but incomplete calcification does not allow observation of some characters that are useful for classification. The earliest occurrence of the genus (*Neomeris cretacea*) is in the Albian of Orizaba (Mexico; Barattolo, 1987).
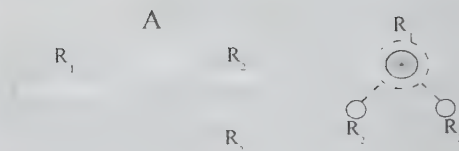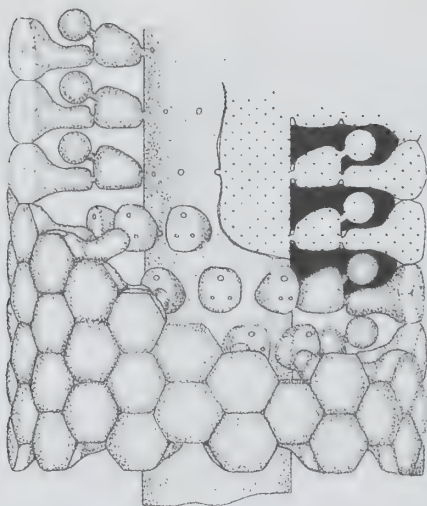
A *Neomeris* subgenus *Larvaria*
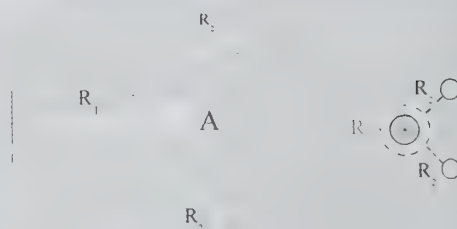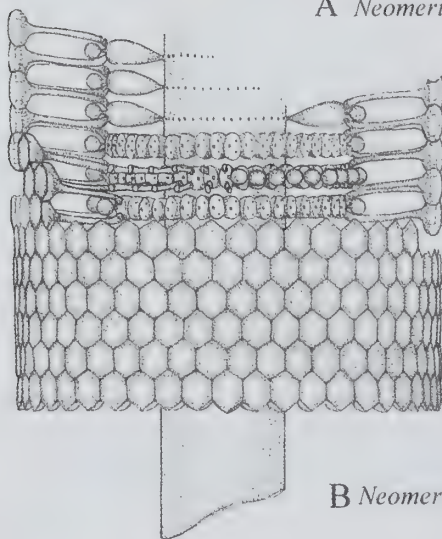


B *Neomeris* subgenus *Drimella*
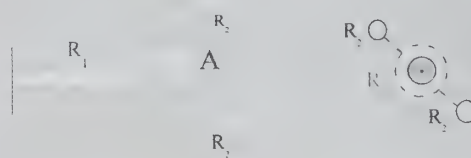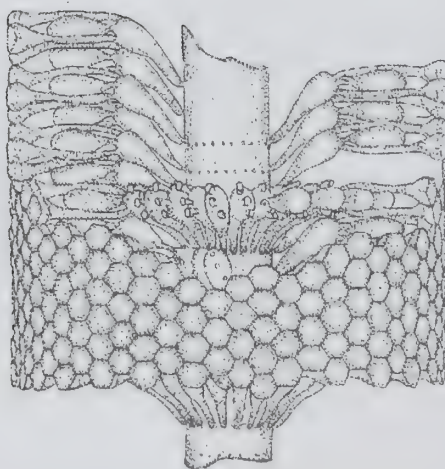


C *Neomeris* subgenus *Neomeris*

**Figs 1A–C** Reconstruction of fossil species belonging to three subgenera of *Neomeris*. **A,** *Neomeris (Larvaria) assurbanipali* Elliott nov. comb.; **B,** *Neomeris (Drimella) drimi* Radoicic 1984; **C,** *Neomeris (Neomeris) cretacea* Steinmann 1899. On the right, the relationships (not to scale) of the primary lateral ($R_1$; broken lined circles), ampulla (A; grey circles) and two secondary laterals ($R_2$; white circles) are shown.

**PLATE 1**

**Fig. 1** *Neomeris (Larvaria) assurbanipali* Elliott *nov. comb.* Oblique section. Lower Cretaceous (Valanginian – Hauterivian), Garagu formation, Erbil Liwa, Iran; V.52032, × 34.

**Fig. 2** *Neomeris (Larvaria) assurbanipali* Elliott *nov .comb.* Detail of the left side of Fig.1, showing the ampulla set on distal end of a primary lateral. Note the secondary lateral set beneath the fertile ampulla. Lower Cretaceous (Valanginian – Hauterivian), Garagu formation, Erbil Liwa, Iran. V.52032, × 54.

**Fig. 3** *Neomeris (Larvaria) assurbanipal* Elliott *nov. comb.* Detail of the lower part of Fig.1, showing the tufts of two phloiophorous laterals making a sort of cortex at the periphery. Lower Cretaceous (Valanginian – Hauterivian), Garagu formation, Erbil Liwa, Iran; V.52032, × 48.

In 1913, Leon & Jean Morellet added greatly to our knowledge of Tertiary fossil species of *Neomeris* and related forms. Their work was based on a rich microflora collected by Munier-Chalmas from the Paris Basin at the end of the 19th century. In addition to documenting new fossil material, they established several neomerid genera (e.g. *Larvaria, Vaginopora, Meminella*) that were later considered as junior synonymous of *Neomeris* (Génot 1980). Deloffre & Génot (1982) gave the following description of *Neomeris*: 'Two orders of branches. Each primary branch bears one fertile ampulla and two (sometimes three in living *Neomeris*) secondary branches. These are set on both sides of the fertile ampulla (*Neomeris s.s.*) or set in a plane located beneath the plane containing fertile ampullae (sub-genus *Larvaria*)'.

Later, Radoicic (1984) established the new subgenus *Drimella*, based on a Late Cretaceous species from Serbia, and gave the following diagnosis: '*Neomeris* with secondary branches laterally located on one side of the fertile ampulla, on vertical or more or less oblique plane. In adjacent verticils, secondary branches can be arranged: in one on the same, and in another on the opposite side of the fertile ampulla, or in each verticil on the same side'.

The subdivision into three subgenera (*Neomeris, Larvaria, Drimella*) was confirmed by Génot (1987). Their structural organisation is illustrated in Fig. 1.

Phylum **CHLOROPHYTA** Pascher, 1914
Class **CHLOROPHYCEAE** Kützing, 1843
Order **DASYCLADALES** Pascher, 1931
Family **DASYCLADACEAE** Kützing, 1843
Tribe **NEOMEREAE** Pia, 1920; emend. Bassoullet *et al.*, 1979
Genus *NEOMERIS* Lamouroux, 1816; emend. Deloffre, 1970

## *Neomeris assurbanipali* Elliott, nov. comb.

1968    *Acroporella assurbanipali* Elliott: 18, pl. 1, fig. 5.

HOLOTYPE.    V.52032 (1), slide.

HORIZON AND LOCALITY. Lower Cretaceous, Valanginian/Hauterivian. Garagu Formation. Well no.116, Kirkuk, Iraq.

REFERRED MATERIAL.    G. F. Elliott Colln., presented 1966.

DESCRIPTION.    The character of the species can be deduced from the single specimen in oblique section (pl. 1 fig. 2). Assessment of

**Table 1**    Main biometrical parameters of *Neomeris assurbanipali* Elliott *nov. comb.* All size parameters are given in mm. *d*: inner diameter of the calcareous skeleton; *D*: outer diameter of the calcareous skeleton; *e*: thickness of the calcareous wall; *pv*: vertical width of primary laterals; *pvd*: vertical width of primary laterals at their distal end; *l*: length of primary laterals; *w*: number of primary laterals per whorl; *h*: distance between two subsequent whorls; *p'*: width of secondary laterals; *l'*: length of secondary pores; *da*: diameter of the ampulla.

|      | This paper       | From Elliott, 1968 |
|------|------------------|--------------------|
| d    | 0.55             | 0.55               |
| D    | 1.4              | 1.36               |
| e    | 0.43             |                    |
| pv   | 0.16 – 0.20      | 0.182              |
| pvd  |                  | 0.156              |
| l    | 0.25             | 0.78               |
| w    | 11 – 12          | 12                 |
| h    | 0.23 – 0.25      |                    |
| p'   | 0.010 – 0.012    |                    |
| l'   | 0.20             |                    |
| da   | 0.11             |                    |
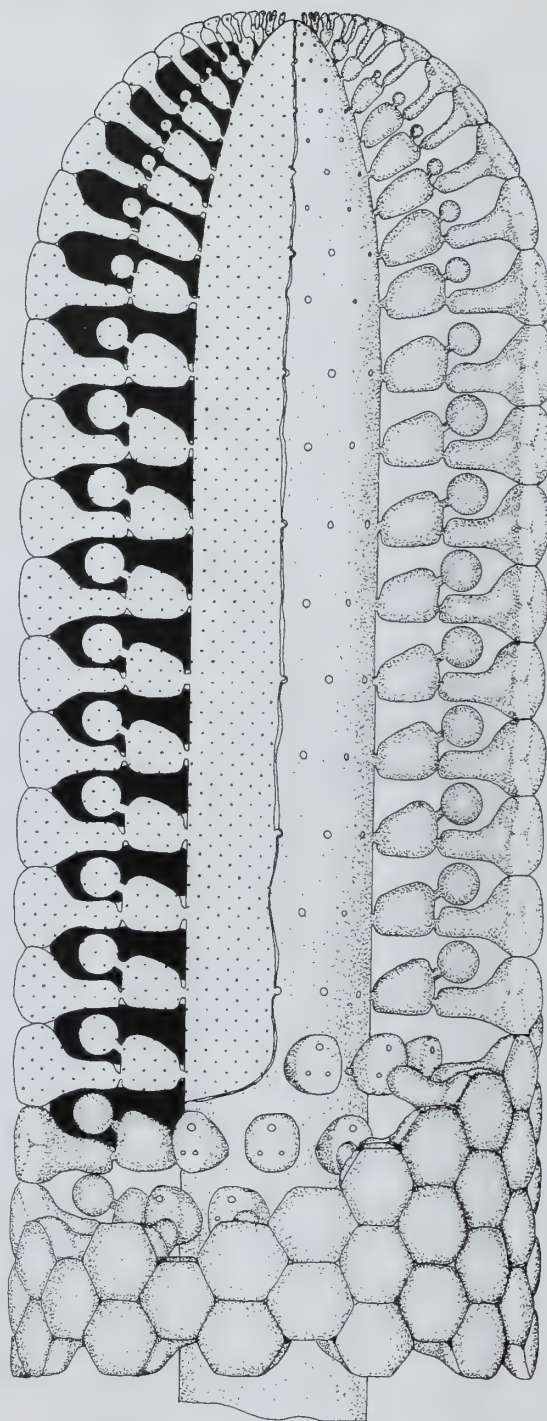


**Fig. 2**    *Neomeris (Larvaria) assurbanipali* Elliott nov. comb. Longitudinal reconstruction of the thallus. Left side: central siphon, primary laterals, secondary laterals, ampullae and calcification (in black) in axial section. Right side: perspective view of the primary laterals, secondary laterals, ampullae and central siphon deprived of calcification. On the left frontal part only the junction of the laterals and the ampullae are drawn. At the base is a perspective view of the cortex built from the secondary laterals drawn in hexagonal meshes ( × 45).

the variability of the species and some qualitative characters such as the shape of thallus, laterals and reproductive organs would have required more abundant material.

The thallus is apparently cylindrical and simple. Primary laterals are arranged in moderately close whorls. Their position between whorls, alternated or in continuity, is not evident. However they are phloiophorous and rather strong, almost perpendicular to the stem axis. The transverse section of the primary pores is rectanglar in the middle part and square in the distal part. The number of primary laterals per whorl can be estimated as 11–12. This value corresponds well with that supplied by Elliott.

Two strong secondary laterals originate from the distal end of each primary lateral. They show a subcylindrical inner part of modest length, 0.11–0.12 mm, and 0.10–0.12 mm in diameter, followed by a part that flares out quickly, so making a cortex at their distal end (pl.1, fig. 3). The two secondary laterals are nearly placed on an horizontal plane, i. e. parallel to the verticillar plane.

Elliott did not identify the twofold laterals, but he interpreted the shape of primary and secondary laterals in longitudinal section as parts of a single lateral. He correctly described the first inner part (primary) as 'a fig- or flask-shaped cavity', and the second outer part (secondary lateral) as 'a slightly curved tube'.

The holotype occasionally shows structures referable to reproductive organs (ampullae: pl.1, fig. 2). The ampulla is set at the distal end of each primary lateral, over the plane where the secondary laterals are placed. It is of spherical shape, 0.11 mm in diameter, joined to the primary lateral probably by means of a short peduncle. The difficulty in observing the reproductive organs can be explained by the fact that most of them were empty and were destroyed after the re-crystallisation of the aragonitic calcareous skeleton. Only those filled by matrix have a chance of being preserved and recognised in thin section.

The calcification consists of a strong calcareous skeleton. It envelopes the primary laterals, the ampullae and the secondary laterals up to their swollen distal end corresponding to the inner edge of the cortex. The smooth and regular inner cavity indicates that calcification probably reached the wall of the central stem. Moreover, in this area the primary laterals open with a reduced pore.

The main biometrical values of the alga are given in Table1.

## PALAEONTOLOGICAL RECONSTRUCTION

The reconstruction in Figs. 2 and 3 takes into account the biometrical values and the morphological characters previously given. The number of pores in a whorl has been chosen to be twelve, and a cortex of hexagonal meshes set horizontally has been supposed. The latter seems to be the most likely arrangement for that number of pores in a whorl and the distance between whorls.

Considering the apex of the thallus, no elements can be deduced from the single specimen at our disposal, and therefore it has been drawn by inference from extant species of *Neomeris* (e.g.. *N. annulata*).

## TAXONOMIC ATTRIBUTION

The species is attributed to the genus *Neomeris* from the evidence of primary laterals in verticils that bear distally two secondary laterals and an ampulla. The fact that the species exhibits two secondary laterals arranged in an horizontal plane beneath an ampulla, allows us to refer *N. assurbanipali* to the subgenus *Larvaria*. The species, if compared with others of the same genus, shows such a combination
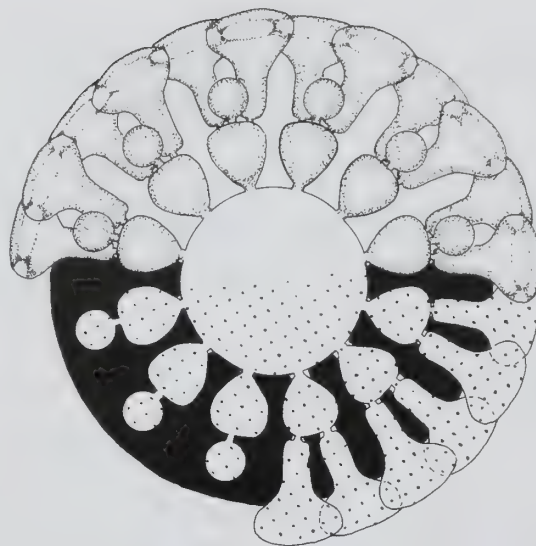


**Fig. 3** *Neomeris (Larvaria) assurbanipali* Elliott nov. comb. Transverse reconstruction of the thallus. Upper half: part of a verticil showing the central siphon, primary laterals, secondary laterals and ampullae without calcification. Lower half, right: transversal section through the primary and secondary laterals, calcification in black. Lower half, left: transversal section through the primary laterals and ampullae, calcification in black ( × 45).

of characters as to maintain the taxonomical validity. In addition *Neomeris (Larvaria) assurbanipali* differs strikingly from all the other counterparts by having a calcareous skeleton that envelops the primary laterals entirely, and seemingly reaches the central stem.

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# Palynological zonation of Mid-Palaeozoic sequences from the Cantabrian Mountains, NW Spain: implications for inter-regional and interfacies correlation of the Ludford/Přídolí and Silurian/Devonian boundaries, and plant dispersal patterns

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## CONTENTS

**SYNOPSIS.** Mid-Palaeozoic strata from the Cantabrian Mountains (north-west Spain) contain rich assemblages of spores, acritarchs and Chitinozoa. Fossil maturation is variable but generally high. The stratigraphical distribution of miospores and cryptospores from four sections through the San Pedro and lower La Vid Formations is sufficiently consistent for the establishment of a sequence of six biozones (including four new biozones). In ascending order the biozones are: 1, *Scylaspora vetusta – S.* sp. B (**V**) Spore Biozone; 2, *Artemopyra brevicosta – Hispanaediscus verrucatus* (**BV**) Spore Biozone; 3, *Coronaspora reticulata – Chelinospora sanpetrensis* (**RS**) Spore Biozone; 4, *Chelinospora hemiesferica* (**H**) Spore Biozone; 5, *Scylaspora elegans – Iberoespora cantabrica* (**EC**) Spore Biozone; 6, *Streelispora newportensis – Emphanisporites micrornatus* (**MN**) Spore Biozone. The *elegans – cantabrica* (**EC**) Spore Biozone is divided into two sub-biozones based on the first appearance of the genus *Aneurospora* and the lower part of the MN Biozone is distinguished as a separate subzone, namely the *Streelispora newportensis – Leonispora argovejae* (**NA**) Spore Assemblage Sub-Biozone (also present in England). The Ludford/Přídolí boundary is probably within the upper part of the *reticulata – sanpetrensis* Spore Biozone, and the *Aneurospora* Sub-Biozone and succeeding **MN** Biozone, allow inter-regional correlation with basal and Lower Lochkovian strata. Comparisons between England, Spain, and North Africa, show that regional differences in spore floras are most marked in the Přídolí. In the Lower Devonian the differences are less pronounced, and the appearance of variants of the genus *Aneurospora* marks a significant event in both the Laurussian and Gondwanan regions, reflecting wide dispersal of their parent plants. Chitinozoans occur throughout most of the sequence and several species have potential for inter-regional correlation e.g. *Ramochitina villosa* (**RS** Biozone) upper part of the *urna* (lower **EC** Biozone) and *Eisenackitina bohemica* (lower **MN** Biozone).

# INTRODUCTION

Because of their abundance and species diversity land plant spores have a much greater potential for the determination of ancient floral regimes than their parent plants. Further, where their fertile parts are known, all Silurian to Lower Devonian (Lochkovian) plants are homosporous with small spores (often *c.* 20 μm, and below 100 μm). Factors which should ensure that their parent plants are widely dispersed. In fact, mid-Palaeozoic spores and marine palynomorphs are found on each of the major drifting continental blocks studied, namely Laurussia and Gondwana. Comparisons of sequences of spores from the Anglo-Welsh area with those from the Cantabrian Mountains and North Africa should aid in the resolution of the nature of these Palaeozoic floras. However, a prerequisite is the study of spore sequences in the three areas. In this study miospores from Southern Britain and the Cantabrian Mountains are studied in detail along with some preliminary work on the chitinozoans of northern Spain. Work on North Africa has been partially published (Richardson & Ioannides, 1973) and additional North African areas are currently being studied. Seward (1931) stated that it is inconceivable that the climate of the Earth was ever uniform, and influences on vegetation might be expected to be profound where crustal pieces drifted through different latitudinal belts. By providing an accurate biozonal framework this work aims to facilitate more accurate comparisons of spore floras in the three areas. The resultant floral dispersal patterns vary through the time interval studied and further work is needed to answer some of the many questions raised.

One of the important features of this study is the completeness of the Přídolí sections in the Cantabrian Mountains in a marine but continentally influenced succession. This probably represents the most complete miospore zonation through the Přídolí Stage. In the continental sections in England there are some of the longest, well-preserved, miospore successions, with a sequence of miospore assemblages from Upper Aeronian to Lower Přídolí and uppermost Přídolí to Lower Lochkovian (Silurian to Lower Devonian). However, there is a gap, equivalent to the upper Lower Přídolí, Middle Přídolí, and lower Upper Přídolí, where no miospore assemblages are known. Between these productive beds of the Lower Devonian (**Aneurospora Subzone** and **MN Zone**) and those from the Lower Downtonian (Lower Přídolí) below, there is, therefore, in England, a considerable gap in the Přídolí spore occurrence. Although there are spores in graptolite-bearing marine sediments in Podolia these spores have been inadequately described and illustrated. The spores illustrated by Shepeleva (1963) from the Lower Devonian of Podolia possibly belong to the **MN Zone** and her species *Lophozonotriletes decoratus* closely resembles *Streelispora newportensis,* the nominal species for the base of the **MN Zone.**

# GEOGRAPHICAL & GEOLOGICAL SETTING (FIG. 1)

The Cantabrian Mountains, in the north and northwest of Spain, extend through the Provinces of Asturias, León, Cantabria and Palencia. Geologically, most of the Cantabrian Mountains belong to the 'Cantabrian Zone' of the Iberian Hercynian Massif and occupies the outermost part of it. The 'Cantabrian Zone' is composed of unmetamorphosed Palaeozoic sedimentary rocks deformed during the Variscan Orogeny. The 'Cantabrian Zone' has been divided into five tectono-sedimentary units (Julivert, 1967), arranged in concentric bands parallel to the 'Narcea Anticlinorium', an arch of Precambrian rocks on the western boundary of the 'Cantabrian Zone' (see Fig. 1). Following to the east of the ' Narcea Anticlinorium' is the 'Folds and Nappes Unit' where the most complete Palaeozoic sequences are found. This Unit occupies the western part of the Asturias and the northern part of the León Provinces. Within this structural unit four sections in a Silurian to Lower Devonian clastic succession have been selected for study.
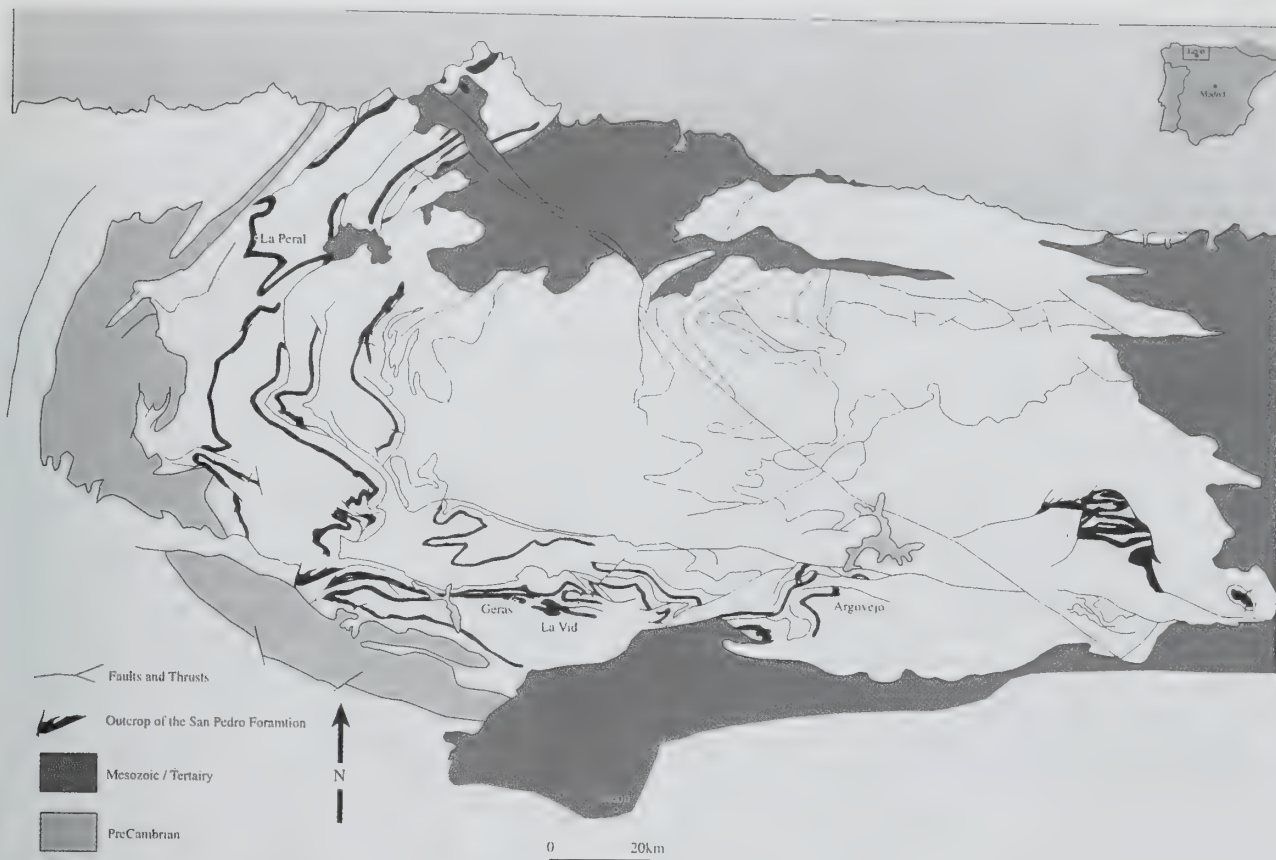
**Fig. 1**  Simplified geology of the Cantabrian Region, NW Spain (based on Rodriguez, 1983).

## San Pedro Formation

This formation was described in two main areas: a, the 'Ferruginous Sandstones of Furada' (Barrois, 1882) on the northern flank of the Cantabrian Mountains, and b, the San Pedro Formation (Comte, 1937) in the south. These two names refer to the Upper Silurian Formations of the 'Folds and Nappes Unit' of the Cantabrian Zone. Three of our sections were originally designated as the San Pedro Formation (Geras de Gordón, La Vid de Gordón and Argovejo). The fourth section was included in the Furada Formation (La Peral). As both formations constitute a single lithostratigraphic unit they are all referred to in the text as San Pedro Formation.

The San Pedro Formation is predominantly sandy and overlies the Formigoso Formation; the latter is Silurian in age. The Formigoso Formation is composed of black shales, with alternating shales and quartzites in the upper part. The San Pedro Formation appears to be in stratigraphical continuity with the underlying Formigoso Formation in the sections near the Precambrian of the 'Narcea Anticlinorium', but the contact is sharp and erosive in the sections situated farther east.

Informally three members can be distinguished in this formation.

*The Lower Member* consists mainly of red ferruginous, coarse-grained sandstones, sometimes with oolites, having cross-trough stratification. At some localities there are conglomeratic beds, with phosphatic, sideritic and silty clasts and intraclasts; some of these clasts have a volcanic origin (Van den Bosch 1969; Suárez de Centi, 1988).

*The Middle Member* is composed of medium to fine grained sandstones with current and wave ripples, and grey to green intensively bioturbated mudstones and siltstones.

*The Upper Member* has fine-grained quartzitic sandstones, with cross stratification, interbedded with dark to black shales.

The San Pedro Formation was deposited in a shallow epeiric sea in intertidal to inner platform conditions (Suárez de Centi, 1988) in a transgressive-regressive cycle (Rodríguez, 1983). In this latter interpretation the middle member represents the deepest conditions.

## Age and biozones of the San Pedro Formation

The age of this formation has been established on macrofauna, microplankton and spores. A macrofauna of brachiopods, molluscs, connularia, trilobites and graptolites has been found, but they are not abundant and are restricted to certain beds (Comte, 1934, 1959; Llopis Lladó, 1958, 1960, 1964; Poll, 1962, 1963, 1970). The lower half of the formation is of Ludlow age, based on brachiopods and connularia (Comte, 1934). In some sections, situated to the west of the 'Folds and Nappes Unit' (see Fig. 1), near one of our localities (La Peral), Poll (1963, 1970) found graptolites 20 to 50 m. below the top of the formation: *Saetograptus fristichi fristichi, S. fr. linearis, S. chimaera salweyi* belonging to the *nilssoni*, *scanicus*, and probably *leintwardinensis* Biozones and indicating a Gorstian to Lower Ludfordian age. The highest part was dated as Lochkovian on its macrofauna (Comte, 1934, 1937, 1959; Poll, 1970).

In contrast to the macrofauna, microplankton and miospores are extremely abundant and well preserved. Microplankton (acritarchs,

chitinozoans) and miospores were extensively studied by Cramer 1964a, b, 1966b, c, 1967, and 1970; by Cramer & Diez 1968, 1975 and 1978a, b; and by Rodriguez 1978a, b, c, 1979, and 1983. Several biozones based on chitinozoans (Cramer & Diez, 1978b) and on acritarchs and miospores (Rodriguez, 1983) have been described. These biozones were established on composite sections and thus they do not constitute formal biostratigraphical units according to the rules of the International Code of Stratigraphic Nomenclature. Instead they constitute respectively, chitinozoans, acritarchs and spore associations, each one arranged in chronological order, ranging from the Upper Wenlock? to Lower Lochkovian. Based on the miospore associations found in the Geras Section, and on correlation with other palynological assemblages found in several different localities, Rodriguez (1983, fig. 13) placed the Silurian/Devonian transition about 5 m below the stratigraphic level adopted in the present work. This author also showed that the boundaries of this formation are highly diachronous (eg. the upper San Pedro Formation is younger in sections to the south and west of the 'Folds and Nappes Unit' than in those closer to the Precambrian Asturian Arch). Argovejo, Geras and La Vid are in the south part of this unit and all these sections have Lochkovian strata at the top.

Chitinozoans of Přídolí and Lochkovian age from the Carazo Formation, of the 'Pisuerga-Carrión Unit', east of the 'Cantabrian Zone', were described by Schweineberg (1987). The Carazo Formation differs in lithology from the San Pedro Formation but, although the precise lateral continuity between these two formations has not been established, the San Pedro Formation also includes sediments of Přídolí and Lochovian age.

# SPORES

## Biozonation (Figs 2–6)

The San Pedro Formation has been sampled in four sections: at Argovejo, Geras de Gordón and La Vid de Gordón (referred to in the text as Geras and La Vid respectively) and La Peral. Productive samples from the La Peral section occur at a lower horizon than in the other sections (Fig. 5). Strata from the underlying Formigoso Formation were sampled in the Argovejo and La Vid sections only. The samples from this formation are practically barren of spores but may contain chitinozoans. The absence of smaller palynomorphs, such as spores, may indicate turbulent to winnowing environments, and possible reworking of at least some chitinozoans. Alternatively, there may be a disconformity either within, or at the top of, the Formigoso Formation (Cramer & Diez, 1978b), and possibly within the lower San Pedro Formation. The La Vid Formation, overlying the San Pedro strata, has been sampled only at the La Vid and Argovejo sections, but all samples taken from shale intercalations in the sandy dolomites were barren.

Four new spore zones, and one subzone, are proposed. These zones, with the exception of the *hemiesferica* Biozone, contain two nominal taxa, at least one of which starts at the base of the zone. The zones are described in ascending order and reference sections are given for the base of each zone, or its lowest known occurrence. In addition, in two sections, possible equivalents of the *Synorisporites libycus – Chelinospora poecilomorpha* (**LP**) Assemblage Spore Biozone (Richardson & McGregor, 1986) occur, and in the La Peral Section the *Artemopyra brevicosta – Hispanaediscus verrucatus*
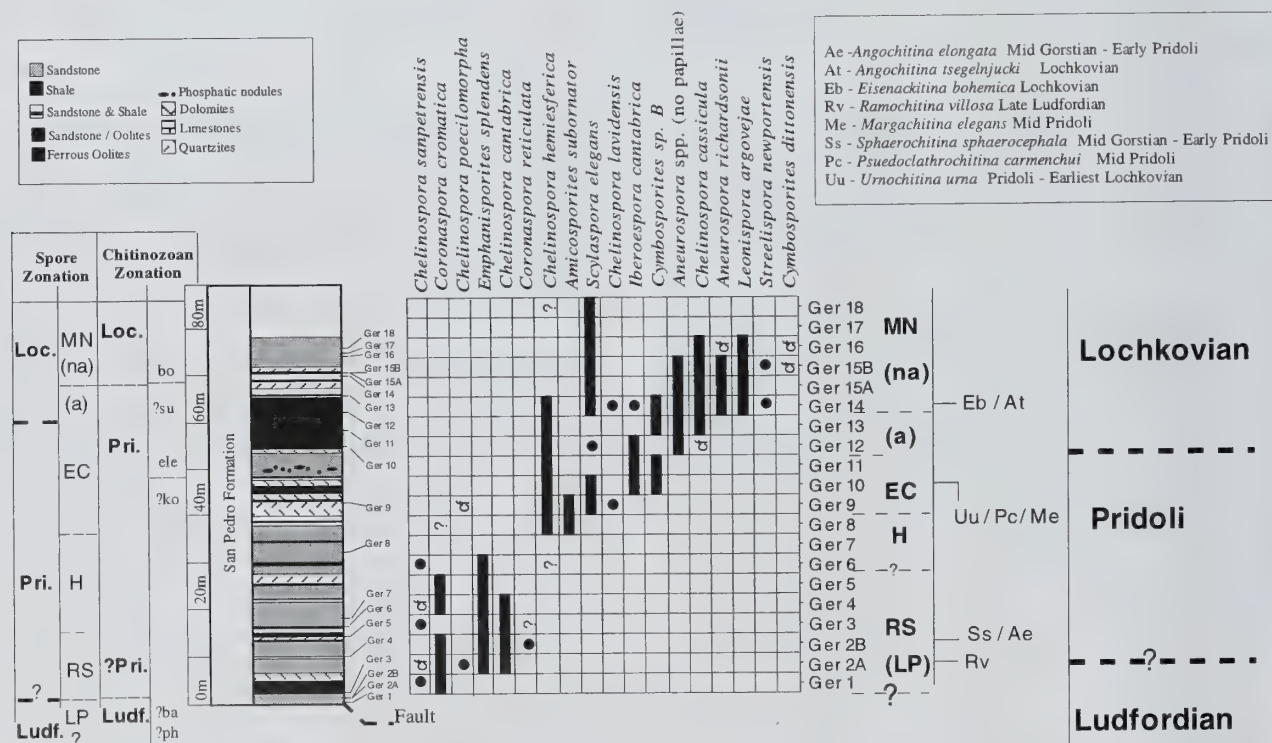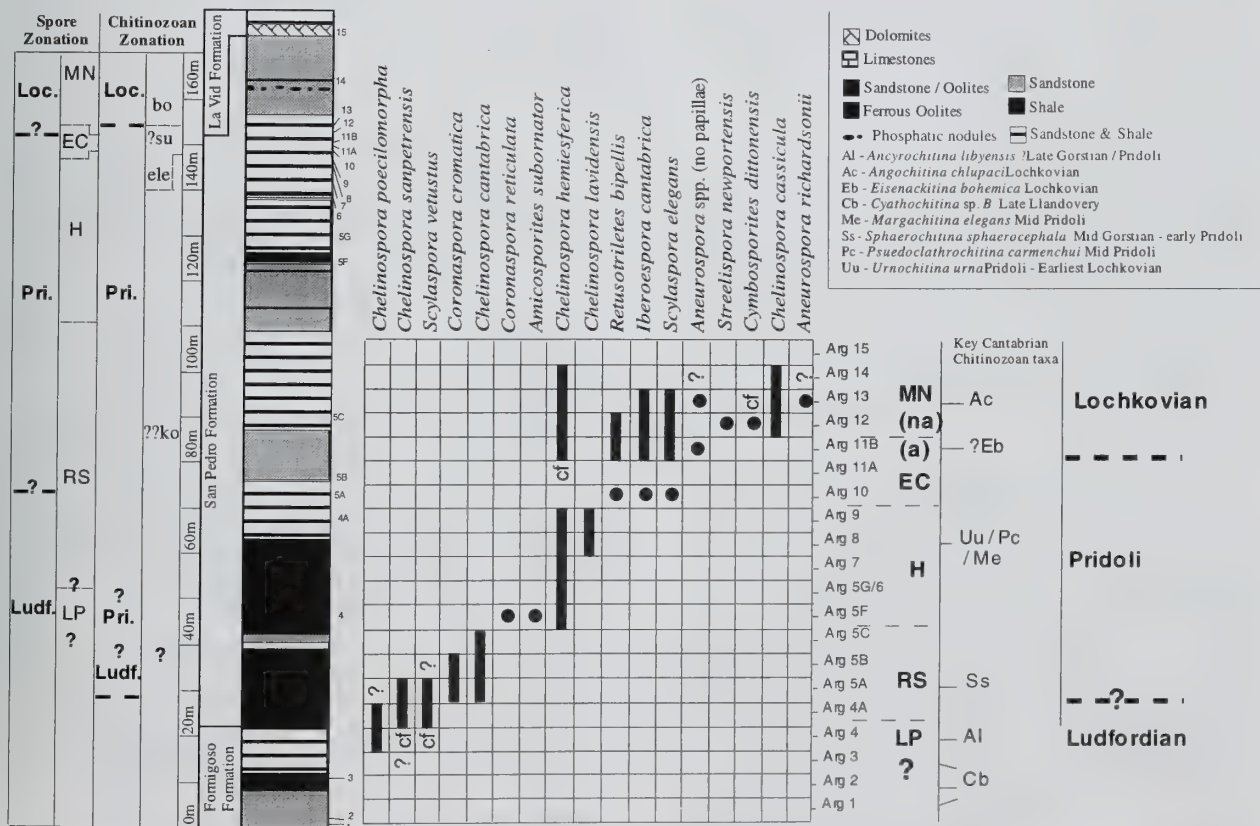


**Fig. 2**  Selected spore distribution at Geras. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi.

(**BV**) Spore Biozone may be present. The latter zone is based on material from the Anglo-Welsh region (Burgess & Richardson, 1991) where the base of the zone, in the type Wenlock area, is recorded in the late *lundgreni* Graptolite Biozone (Lower Homerian, Wenlock).

## *Scylaspora vetusta* – *Scylaspora* cf. *kozlica* (Dufka) (**V**) Spore Assemblage Biozone

DEFINITION. Based on the co-occurrence of the two nominal taxa with *Scylaspora scripta* (Burgess & Richardson, 1995).

NOMINAL SPECIES

*Scylaspora vetusta* (Rodriguez) comb. nov. Rodriguez, 1978b: pl. 1, fig 8.
*Scylaspora* cf. *kozlica* (Dufka) comb. nov. Dufka 1995: pl. 3, figs 10a–10b.

CHARACTERISTIC SPECIES. The species *Ambitisporites abundo* (Rodriguez) comb. nov. and *Concentricosisporites* (?sp.) appear in the upper part of the zone. Within this zone the morphology of *Scylaspora vetusta* is highly variable.

ACCESSORY SPECIES. Long ranging laevigate species such as *Ambitisporites avitus* Hoffmeister 1959, *A. dilutus* (Hoffmeister) Richardson & Lister 1969, *A. warringtonii* (Richardson & Lister) comb. nov., and *Archaeozonotriletes chulus* (Cramer) Richardson & Lister 1969 are present, along with murornate *Synorisporites* sp.

REMARKS. The base of the *Scylaspora vetusta* Biozone is not seen as both the nomimal species occur in the lowest sample of the La Peral section. The upper boundary is defined by the incoming of the nominal species of the succeeding *Artemopyra brevicosta-Hispanaediscus verrucatus* (**BV**) Biozone.

OCCURENCE. Strata of the *S. vetusta* – *S.* cf. *kozlica* Spore Biozone are found only in the La Peral section but the nominal species persist into higher zones in other sections. Higher records are discontinuous and may be, at least in part, due to reworking (La Vid *Coronaspora reticulata* – *sanpetrensis* and lower *Chelinospora hemiesferica* (**H**) Biozones).

AGE. Possibly lower Upper Homerian. Chitinozoa indicate a doubtful Llandovery age and may be reworked.

## *Artemopyra brevicosta* – *Hispanaediscus verrucatus* (**BV**) Spore Biozone

REMARKS. Defined in the Anglo-Welsh area (Richardson & McGregor, 1986, Burgess & Richardson, 1995: 26, text-fig. 8) this zone ranges through the middle and upper parts of the Homerian but is unknown in the lower part of the *lundgreni* Graptolite Biozone at the base of this stage in the type area. The spore zone in the type area is divided into three subzones, namely: *Artemopyra brevicosta*, *Hispanaediscus lamontii*, and *Emphanisporites protophanus* (Burgess & Richardson, 1995). In the La Peral sequence the simultaneous appearance of *A. brevicosta* and *H. verrucatus* (sample LP4) is followed by the occurrence of *Hispanaediscus lamontii* in the next higher sample (LP5, 12 m above) and the nominal species persist into the overlying **RS** Spore Biozone. All of these species are typical of the Homerian, but two (*H. lamonti* and *H. verrucatus*) continue



**Fig. 3**  Selected spore distribution at Argovejo. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis.

into lower part of the *Synorisporites libycus –Chelinospora poecilomorpha* (**LP**) Spore Biozone in the Anglo-Welsh area. Regarding the age of the La Peral samples, there are two main possibilities: the spores represent either an impoverished Gorstian (**LP**) assemblage with reworked fossils from the Homerian, or b, *in situ* Homerian spores. Since older spores may be reworked and deposited inside clasts in younger rocks, they may be preferentially retained, whereas the lower density of contemporary palynomorphs may cause them to be selectively removed by currents.

OCCURENCE.    Found only in the La Peral section.

AGE.    Homerian. In the type Wenlock the *brevicosta* and *lamontii* Sub-Biozones are more or less equivalent to the upper *lundgreni* and *nassa* to lower *ludensis* Graptolite Biozones respectively. There is no chitinozoan evidence for sample LP4 but in the underlying sample (LP3) the chitinozoan species *Conochitina rudda* also indicates a Upper Wenlock to Lower Ludfordian age. Therefore, the chitinozoan evidence fits with an assignment to either the upper *brevicosta – verrucatus* (**BV**) Biozone (Middle to Upper Homerian), or to the succeeding spore zone in the Ludlow.

## *Coronaspora reticulata – Chelinospora sanpetrensis* (RS) Spore Biozone (Figs 3–5)

NOMINAL SPECIES
> *Coronaspora reticulata* sp. nov. *Knoxisporites? riondae* Cramer & Díez 1975 (pars): pl. 1, fig. 17.
> *Chelinospora sanpetrensis* (Rodriguez) comb. nov. Rodriguez, 1978c: pl. 1, fig. 13 (figs i, j, l).

DEFINITION.    Based on the incoming of either of the two nominal species. In some sections the two species appear at the same horizon (La Peral), in others *C. sanpetrensis* appears earlier. The zone represents the interval between the first appearance of the nominal species and the first occurrence of *Chelinospora hemiesferica* (Cramer & Díez) comb. nov.

ACCESSORY SPECIES.    *Chelinospora poecilomorpha*, *Coronaspora cromatica*, *Emphanisporites splendens*, *Chelinospora cantabrica*.

REMARKS.    This biozone is present in all four sections. In the La Peral section the base lies above a thick sandstone in sample 6, c.71 m above the base of the San Pedro Formation. However, in the Argovejo section several species that occur together in the lowest RS Spore Biozone in the other samples follow one another in sequence. This may mean that the oldest part of the zone is seen in the Argovejo sequence. In all sections, however, *Chelinospora cantabrica* appears a little above the first appearance of *C. sanpetrensis*, which suggests that all sections begin at a similar stratigraphical level. The concurrence of the two species may form a useful sub-biozone.

Current data (see also Richardson & McGregor, 1986) indicate that trilete spores, with a regular distal reticulum of even lacunae and well-developed muri, first appear in the Přídolí. However, precise corroboration is lacking, and spore/chitinozoan assemblages from the lower parts of the Cantabrian Mountains sections studied are often poor. Consequently, the exact relation of this sculptural event to the Ludfordian/Přídolí boundary in the Cantabrian Mountains is not clear. Distally reticulate spores first appear in the **RS** Spore Biozone and the spore evidence indicates an Upper Gorstian age for the base of the biozone. Other rare taxa include *Insolisporites* sp. (Pl. 3, fig. 3) and similar taxa are found in Britain in the Ludlow. Chitinozoans in Ger 2A indicate an Upper Ludfordian age and consequentely the upper part of the **RS** Spore Biozone is probably of Přídolí age.

REFERENCE SECTION.    La Peral, Cordillera Cantabrica, Province of

Asturias, NW Spain. The 'base' of the zone is between 49 and 71 m above the base of the San Pedro Formation. The strata in this 22 m interval are dominated by red sandstones and were not sampled. The zone is at least 22 m thick in the La Peral section.

DISTRIBUTION.    La Peral, Geras, La Vid and Argovejo sections. In the Argovejo sequence the thickness of the zone is uncertain due to a 40 m interval where samples are barren. In the other sections the thickness of the zone is around 15–25 m.

ARGOVEJO SECTION.    The lowest eleven samples are barren or do not contain diagnostic palynomorphs. In sample ARG/4 *poecilomorpha* occurs with cf. *sanpetrensis* and may indicate the presence of the upper part of the **LP** Biozone ( Upper Ludfordian in England and Wales). Chitinozoa from the same sample are long ranging from Upper Gorstian to Přídolí and therefore do not conflict with the presence of the upper **LP** Spore Biozone but are insufficiently precise.

GERAS SECTION.    *Chelinospora sanpetrensis*, one of the nominal species of the **RS** Spore Biozone, occurs in the basal sample (Ger 1) of the Geras section. *Chelinospora poecilomorpha* and *Stellatispora inframurinatus* var. *cambrensis* appear in the overlying samples (Ger 2A and Ger 3 respectively) and are also found in the upper Gorstian and Ludfordian of England and Wales but are absent from the succeeding Downtonian there. The presence of the chitinozoan *Ramochitina villosa* indicates a Late Ludfordian age for sample Ger 2A within the **RS** Biozone. *Emphanisporites splendens* appears in Ger2A to Ger6. This species is found in North Africa in association with typical lower Downton (Lower Přídolí) species in the upper part of its known range there. Thus, at least part of the **RS** Spore biozone is of Upper Ludfordian age and, on present evidence, the Ludfordian/Přídolí boundary probably occurs within the higher parts of the **RS** Biozone. The Geras section is faulted at the base and no further samples were collected below Ger 1. *Coronaspora primordiale* (Pl. 6, fig. 3) occurs rarely in samples Ger 2B and Ger 3, but in the Argovejo and La Peral sections is found sporadically only in the overlying **H** Biozone. *Emphanisporites* spp. (eg. Pl. 2, fig. 9) occur rarely in sample Ger 2B and also extend into the overlying **H** Biozone in the La Peral section. Other species typical of the Homerian and Gorstian occur erratically in this section and are most probably reworked, eg. *Hispanaediscus lamonti*.

LA VID SECTION.    The lowest productive sample in the San Pedro Formation is LV 6, which belongs to the **RS** Biozone. However, spores similar to S. *libycus* and indistinguishable from *C. poecilomorpha* (nominal species of the **LP** Biozone) occur. In England and South Wales these species die out near the top of the Ludfordian. Part of the **RS** Biozone is probably, therefore, Ludfordian and may be equivalent to the *libycus – poecilomorpha* Biozone of the Anglo-Welsh area. However, in the Cantabrian sections examined the nominal species of the **LP** Biozone are erratically distributed. Reworking is also evident in this part of the sequence and taxa typical of the Homerian and Lower Gorstian occur there. These finds are associated with an incursion of thick sandstones.

AGE.    Ludfordian to lowermost Přídolí. Chitinozoa in samples from the **RS** Biozone in the Argovejo, Geras and La Peral sections mainly have a long range, from Mid-Gorstian to Lower Přídolí.

## *Chelinospora hemiesferica* (H) Spore Interval Biozone (Figs 2–5)

NOMINAL SPECIES
> *Chelinospora hemiesferica* (Cramer and Díez) comb. nov.; Cramer and Díez 1975: pl. 2, figs 34–36, (Pl. 9, figs 3, 5).
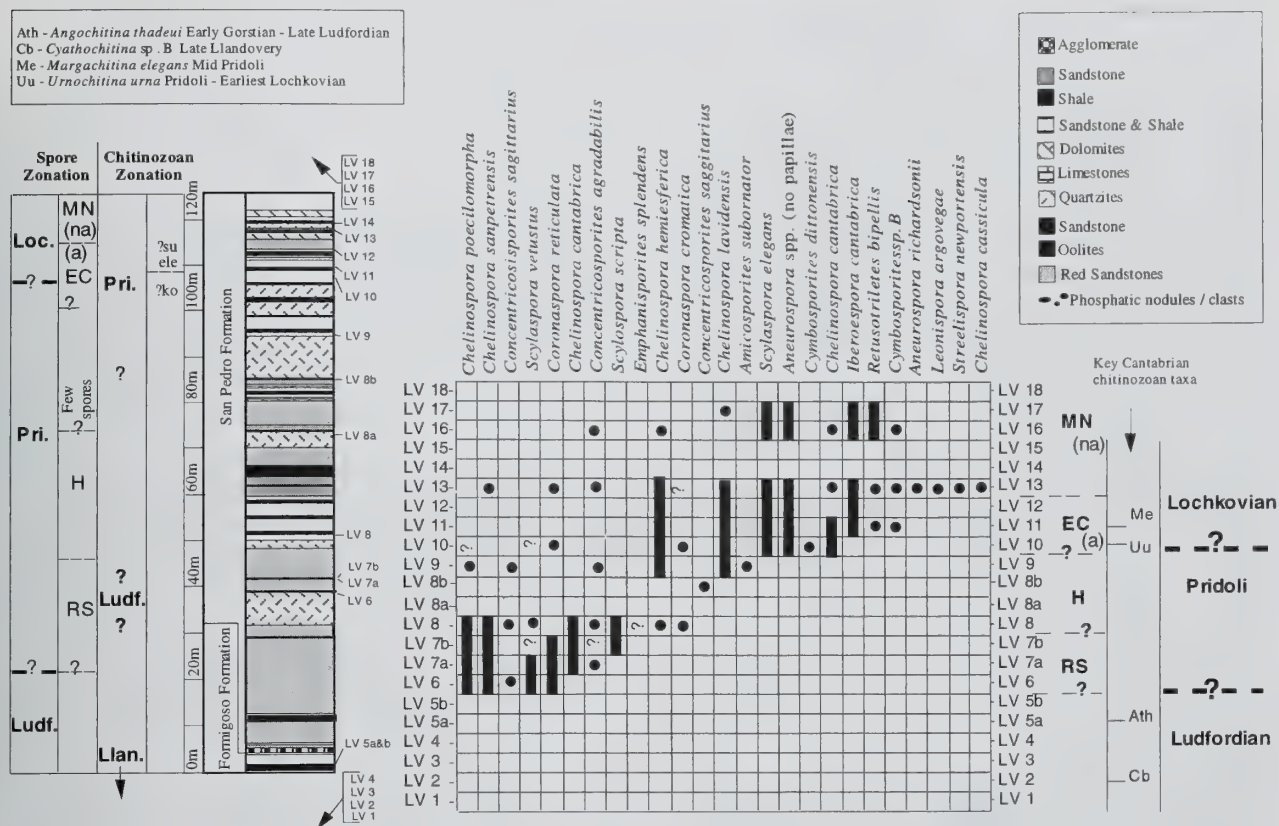
Ath - *Angochitina thadeui* Early Gorstian - Late Ludfordian
Cb - *Cyathochitina* sp . B Late Llandovery
Me - *Margachitina elegans* Mid Pridoli
Uu - *Urnochitina urna* Pridoli - Earliest Lochkovian

**Fig. 4** Selected spore distribution at La Vid. Chitinozoan zonation after Verniers *et al.* (1995): **su**: superba, **ele**: elegans, **ko**: kosovensis.

*Coronaspora subornata* (Cramer and Díez) comb. nov.; Cramer & Diez 1975: pl. 1, fig. 7, (Pl. 8, fig. 7).

REFERENCE SECTION. San Pedro Formation, Geras, Province of León, Cordillera Cantabrica, NW Spain. The base of the zone is between samples Ger 5 and 6, and the base of sample 6 is c.16.2 m above the base of the section. The zone is about 22 m thick in the Geras section.

DEFINITION. The base of the zone is based on the first appearance of *C. hemiesferica* (Cramer & Diez). In the lower part of the zone *Chelinospora sanpetrensis* (Rodríguez), *Coronaspora reticulata* sp. nov. and *Emphanisporites splendens* (Richardson & Ioannides, 1973) persist. This biozone represents the interval between the appearance of the nominal species and the first occurrence of *Scylospora elegans* and *Iberoespora cantabrica* (EC) Biozone.

ACCESSORY SPECIES. *Coronaspora subornata* (occurs erratically within the zone), *Chelinospora canistrata* sp. nov. *Concentricosisporites agradabilis* (Rodriguez) Rodriguez, 1983. All the accessory spores have been found in three of the four sections.

REMARKS. *Chelinospora hemiesferica* (Cramer & Diez) shows considerable variation and a morphological series can be traced in these sections. *C. hemiesferica* (Silurian, Přídolí) has narrow geniculate muri and higher in the zone is accompanied by *C.* cf. *hemiesferica* with broader muri, and then *C. lavidensis* and *C. media,* which both have wide lumina and occur along with typical Lower Devonian (Lochkovian) species *Chelinospora cassicula* Richardson & Lister. So far the variant *C.* cf. *hemiesferica* has been found in three of the

four sections: Geras (**EC** Biozone), La Peral (**H**, and **EC** Biozones), and La Vid (upper **EC** (*Aneurospora* Sub-Biozone), lower **MN** Sub-Biozone).

AGE. Lower and Middle Přídolí. The chitinozoan *Urnachitina urna* occurs in the basal sample (LP10) of the *hemiesferica* Biozone in the La Peral section, *U. urna* has a range from Přídolí to lowermost Lochkovian.

## *Scylaspora elegans* – *Iberoespora cantabrica* (EC) Spore Assemblage Biozone (Figs 2–5)

NOMINAL SPECIES
  *Scylaspora elegans* sp. nov. (Pl. 5, figs 2–4, Pl. 6, fig. 8).
  *Iberoespora cantabrica* Cramer & Diez 1975: pl. 2, figs 24, 26–28 (Pl. 6, fig. 4; Pl. 7, fig. 4).

REFERENCE SECTION FOR BASE OF BIOZONE. La Vid section, Cantabrian Mountains, Province of León, NW Spain. The lowest occurrence of *Scylaspora elegans* was found in sample LV10, *c.* 102 m above the base of the section.

DEFINITION. The base of the zone is defined by the incoming of one, or both, of the nominal species. Usually *Iberoespora cantabrica* occurs stratigraphically above *S. elegans*. The first appearance of *Aneurospora* spp., lacking proximal papillae, defines a sub-biozone in the upper part of the zone.

ACCESSORY SPECIES. *Retusotriletes bipellis* Rodriguez, 1978c, *Cymbosporites* sp. B, and several *Chelinospora* morphs (variants)

with narrow and coarse muri and an irregular reticulum are common accessory spores. *Retusotriletes coronadus* (Rodriguez, 1983: pl. 8, fig. 1) appears in the lower part of the zone.

REMARKS. The upper part of the **EC** Biozone (*Aneurospora* Sub-Biozone) is recognisable in England (Hereford and Worcester) in the Raglan Marl Formation below the first appearance of the **MN** Biozone in the St. Maughans Formation (Richardson, Rodriguez & Sutherland, 2000). In the La Vid section (Fig. 4) the earliest definite specimens of *Scylaspora elegans* and *Aneurospora* spp. occur together, consequently the lower part of the **EC** biozone has not been found there.

OCCURENCE. The zone is found in all four sections.

AGE. Upper Přídolí to lowermost Devonian. The appearance of the genus *Aneurospora* is probably close to the base of the Devonian (Richardson, Ford & Parker 1984; Richardson, Rodriguez & Sutherland, 2000). Chitinozoans in the lower **EC** Biozone are of Middle Přídolí age (basal **EC**, La Peral, lower **EC**, Geras and La Vid sections). The same chitinozoans indicating a mid-Přídolí age (*Margachitina elegans*) and Přídolí to earliest Lochkovian age (*Urnochitina urna*) are both present in the upper part of the **EC** Biozone (*Aneurospora* Sub-Biozone) and in the top of the underlying **H** Biozone.

## *Aneurospora* spp. (A) Sub-Biozone (Figs 2–5)

REFERENCE SECTION FOR BASE OF SUB-BIOZONE. Upper San Pedro Formation, La Vid section, Cantabrian Mountains, NW Spain. The lowest occurrence of *Aneurospora* spp. was found in sample 10, *c.* 106 m above the base of the section.

DEFINITION. Appearance of the genus *Aneurospora* without proximal papillae. Represents the interval between the appearance of *Aneurospora* and the incoming of *Streelispora newportensis* of the succeeding zone.

ACCESSORY SPECIES. Spores of the *Chelinospora hemiesferica* (Cramer & Diez) complex, *C.* cf. *hemiesferica*, *C. cassicula* Richardson & Lister 1969, *C. lavidensis* sp. nov., *C. media* sp. nov., *Cymbosporites* sp. B, and *Retusotriletes coronadus* s.s.

OCCURENCE. Found in all four sections in the Cantabrian Mountains.

AGE. Earliest Devonian (Lower Lochkovian), assessment based on comparison with sections in the Lower Old Red Sandstone of England.

## *Streelispora newportensis – Emphanisporites micrornatus* (MN) Spore Biozone Richardson & McGregor, 1986 (Figs 2–4); *Streelispora newportensis – Leonispora argovejae* Spore Assemblage (NA) Sub-Biozone

NOMINAL SPECIES
*Streelispora newportensis* (Chaloner & Streel) Richardson & Lister 1969: pl. 41, figs 3–6 (Pl. 7, fig. 8).
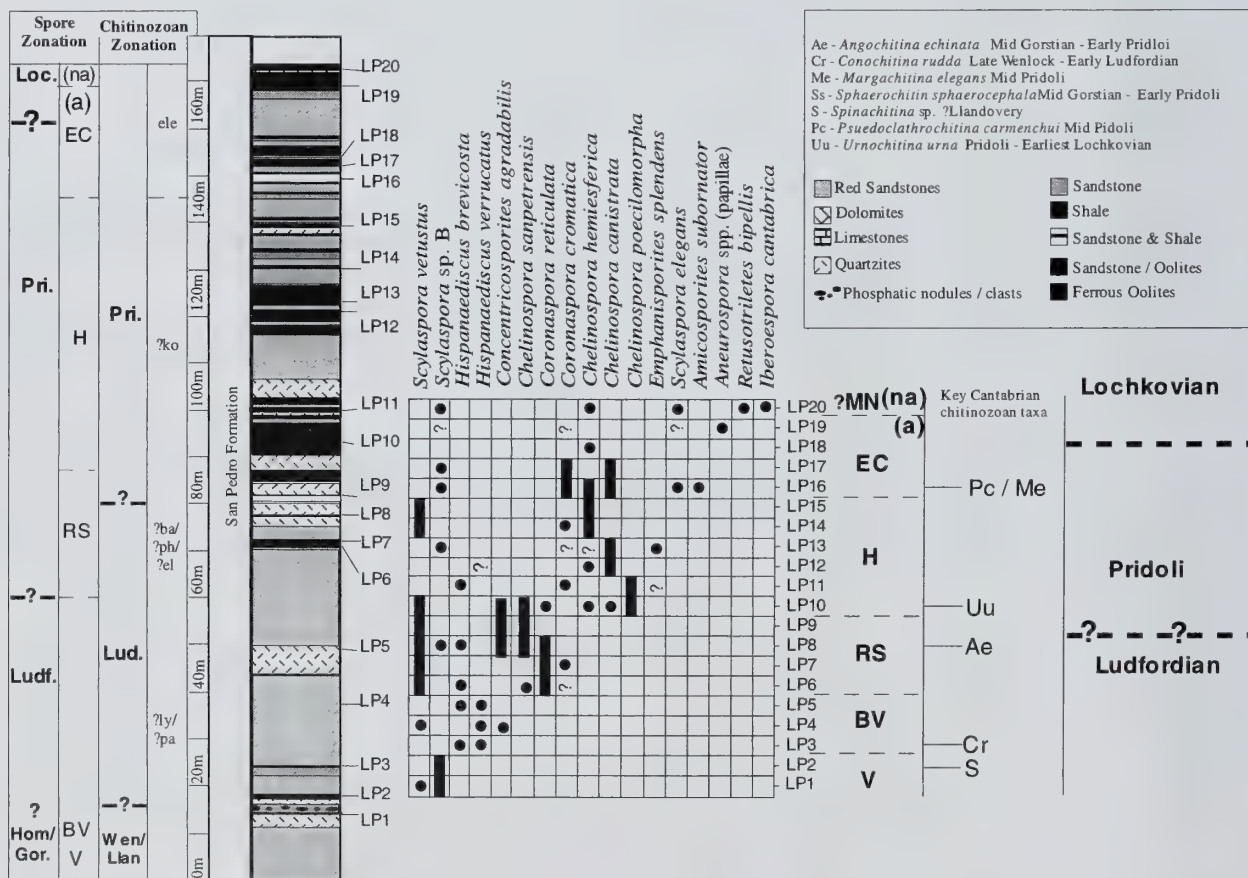


Fig. 5   Selected spore distribution at La Peral. Chitinozoan zonation after Verniers *et al.* (1995): **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi, **el**: elongata, **ly**: lycoperdoides, **pa**: pachycephala.

*Leonispora argovejae* Cramer & Diez 1975: pl. 1, fig. 3 (Pl. 7, fig. 5).

REFERENCE SECTION FOR BASE OF SUB-BIOZONE.  San Pedro Formation, Geras section, 70.1 m above the base of the section (sample Ger14).

DESCRIPTION.  First appearance of tripapillate species of the *Aneurospora – Streelispora* complex (*S. newportensis* and *Leonispora argovejae*), the non-papillate species *A. richardsonii*, and the murornate and apiculate patinate species, *Chelinospora cassicula*, *C. media* and *Cymbosporites dittonensis*. Spores with a well-developed zona first appear within the zone. Persistence of *R. coronadus* and appearance of spores with curvatural spines and a narrow curvatural zona (*Breconisporites*? sp. C; Pl. 4, fig. 3) at the base of the **MN** Biozone.

ACCESSORY SPECIES.  In Britain the **MN** Biozone is divided into three sub-biozones (Richardson, Ford & Parker 1984). With the exception of *A. richardsonii* (Rodriguez) comb. nov., *R. coronadus* Rodriguez 1983, and *Breconisporites*? sp. C all the species listed above occur also in the lower **MN** Sub-Biozone of the Anglo-Welsh area and consequently the **NA** Sub-Biozone can be used there also.

REMARKS.  The **MN** Biozone is widely distributed. It is found in England, Scotland, Wales, Belgium, Poland, Podolia (Ukraine), Baltic States, northwest Spain and North Africa (Libya & Morocco), northwest and southern China (Richardson & McGregor, 1986), Poland (Turnau, 1986), and the U.S.A. (Wood, pers. comm.).

Rare specimens of *Telisporites* sp. A and *Emphanisporites* cf. *decoratus* (Pl. 3, figs 2, 6) occur in the highest productive sample of the La Vid section, also high in the Argovejo section (sample Arg 14). *Raistrickia* sp. (Pl. 3, fig. 4), a taxon not found in England and Wales at this level, also occurs in the Geras section.

OCCURENCE.  The **MN** Biozone occurs in the upper San Pedro Formation in the Argovejo, Geras, and La Vid sections.

AGE.  Lower but not lowermost Devonian (Lochkovian) based on spores, probably lowermost Devonian based on chitinozoans.

## AGE OF THE BIOZONES AND INTER-REGIONAL PALYNOLOGICAL CORRELATION

Palynological correlation reveals several anomalies between the ages based on chitinozoans and those on spores in three of the four sections examined from the Cantabrian Mountains. There is evidence for considerable reworking in three of the sections. In other parts of the sections the data are consistent between the two fossil groups and the sequence of spore zones can be traced throughout the study area. All but the lower two zones in La Peral are found in at least three localities.

In spite of regional differences there are a number of species that are found both in the Silurian type area of England and south Wales and the current area of study. Of the four sections, that at La Peral is farthest offshore and perhaps represents a more continuous spore sequence less disturbed by reworking than the sediments in the Argovejo, Geras and La Vid sections where the San Pedro Formation is marginal marine in part. For this reason the La Peral section is taken as our basis for correlation of our sections with those from the Anglo-Welsh type area. and, although the preservation of the spores is not as good in the La Peral section, it is nevertheless sufficient for correlation with Britain up to the *Aneurospora* Sub-Biozone.

## La Peral Section (Figs 5, 6)

**LP1, LP2**. These samples belong to the lowermost part of the San Pedro Formation . The assemblages are relatively poor with only thirteen cryptospore and miospore taxa recorded so far. (N.B. the spore range charts are not published in full at this time and only those important for local zonation are included in Fig. 5). Chitinozoans indicate a Llandovery age for this interval and, although some of the spore species also occur in the Upper Llandovery they are long ranging forms. Sculptured spores e.g. *Scylaspora* spp. have not been found in the type area below the upper part of the Homerian Stage. This discrepancy between the spore and chitinozoan data may be due to reworking of the chitinozoan *Spinachitina,* as the transition from the underlying formation to lower part of the San Pedro Formation constitutes a regressive-transgresive cycle across the whole area. Thus, the lower part of the San Pedro Formation in this area may represent a transgressive cycle where reworking may be prevalent. Reworking of Upper Llandovery spores would be practically invisible in impoverished younger assemblages as the spore records of *Ambitisporites* spp. found in these samples range from the Upper Aeronian (Llandovery) into the Devonian.

**LP3–LP5**. This assemblage of sculptured cryptospores includes typical Upper Homerian and Lower Gorstian forms such as *Artemopyra brevicosta, A. radiata, Hispanaediscus lamontii* and *H. verrucatus.*

**LP6–LP9**. *Stellatispora inframurinata* var. *cambrensis* and spores similar to *Chelinospora obscura,* appear in LP6 and they are both typical Gorstian species. The miospore species *Concentricosisporites sagittarius* (LP8) first occurs at the base of the Ludlow Series (basal Gorstian) in the type area. All three taxa are key species in the Anglo-Welsh area. This age is consistent with that indicated by chitinozoans in sample LP8 dated as Middle Gorstian to Middle Přídolí age. *Stellatispora inframurinata* is used as a zonal species in England and Wales and is found in the Upper Gorstian and Ludfordian stages. With the exception of *S. inframurinata,* none of these forms has been found above the Ludlow in the type area. In sample LP 10 (10 m higher than LP 8) *C. hemiesferica* occurs for the first time, marking the base of our **H** Biozone.

**LP12–LP16**. The first appearance of *Amicosporites splendidus* may mark either the uppermost Ludfordian or the lowermost Přídolí. There were no chitinozoans in sample LP12 but in the overlying sample (LP16) chitinozoans typical of the Middle Přídolí have been found.

**LP19**. According to our research the genus *Aneurospora* marks a level at, or near, the base of the Devonian. Unfortunately chitinozoan evidence is limited and suggests a Lower to Middle Přídolí age. However, in all the other sections studied the *Aneurospora* Sub-Biozone is followed by the **MN** Biozone, which is found only in Lower, not basal, Lochkovian. LP20 may belong to the MN Biozone but lacks the nominal species.

## SPORE BIOZONES

*Scylaspora vetusta* (**V**) **Spore Biozone.** This biozone has been found only in the La Peral Section samples (LP1, LP2). The assemblage is limited but contains *Scylaspora vetusta* and *Retusotrileter abundo.* Both these species were found in North Africa (Richardson & Ioannides, 1973) but the latter occurs 60 m above Wenlock/basal Ludlow graptolites. *Scylaspora* and *Synorisporites* sp. indicate an age not older than late Lower Homerian.
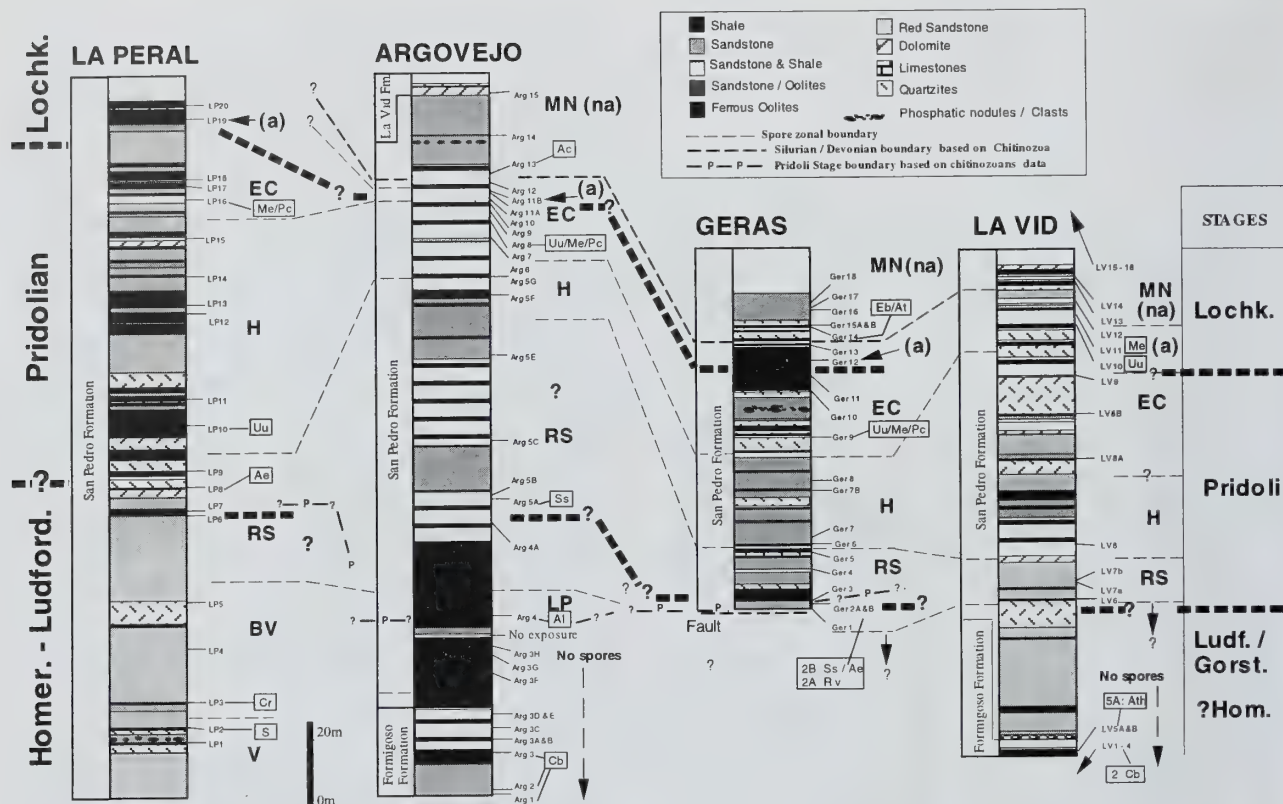
**Fig. 6** Correlation of Cantabrian sections. Spore zonation new, except for LP Biozones after Richardson & McGregor (1986), **MN** Biozone after Holland & Richardson (1977) and Richardson & McGregor (1986), and **BV** Biozone after Burgess & Richardson (1995); **MN**: micrornatus – newportensis, **(na)**: newportensis – argovejae Subzone, **(a)**: Aneurospora Subzone, **EC**: elegans – cantabrica, **H**: hemisphaerica, **RS**: reticulata – sanpetrensis, **LP**: libycus – polymorpha, **BV**: brevicosta – verrucatus, **V**: vetusta. Key Cantabrian chitinozoan taxa: **Ac**: *Angochitina chlupaci* Lochkovian, **Ae**: *Angochitina echinata* Mid Gorstian – Lower Přídolí, **Al**: *Ancyrochitina libyensis* Late Gorstian? – Lower Pvrídolí, **Ath**: *Angochitina thadeui* Lower Gorstian-Late Ludfordian, **At**: *Angochitina tsegelnuki* Lochkovian, **Cb**: *Cyathochitina* sp. B Late Llandovery, **Cr**: *Conochitina rudda* Late Homerian-Lower Ludfordian, **Eb**: *Eisenackitina bohemica* Lochkovian, **Me**: *Margachitina elegans* Mid Přídolí. **Pc**: *Pseudoclathrochitina carmenchui* Mid Přídolí, **Rv**: *Ramochitina villosa* Late Ludfordian, **Ss**: *Sphaerochitina sphaerocephala* Mid Gorstian to Lower Přídolí, **S**: *Spinachitina* sp. Llandovery?, **Uu**: *Urnachitina urna* Přídolí-earliest Lochkovian.

*Artemopyra brevicosta – Hispanaediscus verrucatus* (**BV**) **Spore Biozone (Burgess & Richardson 1995).** Both the nominal species are found in samples LP3 and LP5. The fact that *Hispanaediscus lamontii* also occurs in the latter sample may indicate that the junction between the *A. brevicosta* and *H. lamontii* Sub-Biozones lies between these two samples. In south Wales this sub-zonal boundary occurs in the Middle Homerian between the *lundgreni* and *nassa* Graptolite Biozones.

*Chelinospora reticulata – C. sanpetrensis* (**RS**) **Spore Biozone.** This biozone is represented in all four sections. In the La Peral section both the nominal species appear together in sample LP6. Neither species has been found in the type area of England and Wales. However, the **RS** assemblages include *Concentricosisporites sagittarius* and *Stellatisporites inframurinatus* var. *cambrensis* first found in the Lower and lower Upper Gorstian respectively, and spores similar to *Chelinospora obscura* in the Middle Gorstian. All of these species can occur together in the lower part of the *cambrensis* Sub-Biozone. On current data, therefore, we tentatively, regard the lower boundary of the **RS** Biozone as lower Upper Gorstian, approximately lower *incipiens* Graptolite Biozone.

*Chelinospora hemiesferica* (**H**) **Spore Biozone.** The base of the *hemiesferica* Biozone is found in sample LP 10 in the La Peral section. Associated spores are mainly found in the Cantabrian Mountains and North Africa. Several species, however, also occur in the Anglo-Welsh area. One of these, *Chelinospora poecilomorpha* occurs throughout the Ludlow Series in south Wales but has not been found in the Lower Přídolí there. In North Africa this species has a similar range and occurs with *Emphanisporites splendens*, a co-occurrence also found in LP9. In sample LP12 *Amicosporites splendidus* occurs and this species is also found in the uppermost Ludfordian to Downtonian (Lower Přídolí) in England but is rare there. The base of the biozone is placed tentatively, therefore, in the Lower Přídolí but could be also of latest Ludfordian age.

*Scylaspora elegans – Iberoespora cantabrica* (**EC**) **Spore Biozone.** The first appearance of *Scylaspora elegans* occurs in the La Peral section in sample LP 16 coeval with chitinozoans typical of the Middle Přídolí. This is consistent with chitinozoan finds in the sections of Argovejo (Arg 8), Geras (Ger 10), and La Vid (LV 10, LV 11). The base of the zone is therefore placed in the Middle Přídolí with some confidence.

*Aneurospora* (**A**) **Spore Sub-Biozone.** The first occurrence of this genus is found in three of the four sections studied: La Peral (sample

LP19), Geras (sample Ger 12) and La Vid (sample LV 10). This spore event occurs in England in sections from Hereford and Worcester in strata below the **micrornatus – newportensis (MN)** Zone. Although the *Aneurospora* Sub-Biozone in the Cantabrian Mountains occurs a little below (*c*. 5 m) the occurrence of the typical Lochkovian chitinozoans *Eisenackitina bohemica* and *Angochitina tsegelnjucki* (Geras), we regard the base of this Sub-Biozone as close to the Silurian/Devonian Boundary (Richardson, Rodríguez & Sutherland, 2000). This correlation is based partly on comparisons with material from Podolia described by Arkhangel'skaya (1980). In Podolia, below the base of the equivalents of the MN Biozone (Chortkov Group), there is distinct spore assemblage in the Mitkov Formation (Borshchov Group). This lower assemblage probably contains non-papillate spores of the genus *Aneurospora* and is above the first occurrence of the graptolite *Monograptus uniformis uniformis* providing support for the idea that the *Aneurospora* **(A)** Sub-Biozone is Devonian. Based on the distribution of key chitinozoan species, Paris & Grahn (1996) used

the base of *Monograptus uniformis uniformis*, the higher of the two critical graptolite subspecies, to mark the base of the Devonian. In particular *Eisenackitina bohemica*, also found by us in the Cantabrian Mountains, and other restricted chitinozoan species occur in the upper Tajna Formation along with *M. uniformis uniformis*. Although it is difficult to be certain, because of the nature of the spore illustrations (Arkhangel'skaya, 1980), this Lower Podolian spore assemblage appears to include non-papillate species/varieties of *Aneurospora* and may, therefore, be equivalent to the *Aneurospora* Sub-Zone. Assemblages with tripapillate spores (*Aneurospora/Streelispora*?) occur in the Chortkov Group *c*. 70 m above the Mitkov assemblage. The Silurian/Devonian Boundary is currently placed at the first appearance of *M. uniformis angustidens* at base of the Borshchov Group (Tajna Formation, Nikiforova, 1977) but no spore assemblages have been described from the lower part of the Borshchov Group. Even so, the position of the Silurian/Devonian boundary as determined by Paris & Grahn seems reasonable from the spore evidence currently available.



**Fig. 7** Přídolí palaeotectonic-palaeogeographic map. Simplified from Ziegler (1988).

## LAURUSSIA – GONDWANA SPORE DISTRIBUTION PATTERNS (FIGS 7–9)

Upper Silurian and Lower Devonian spore floras are diverse and homosporous but little is known of their geographical dispersal. Silurian palaeogeographical maps show Europe and North America at low latitudes, between the Tropic of Capricorn and the equator (Witzke & Heckel, 1988), separated by an ocean from Gondwana (with Iberia in close proximity on its northern flanks) in higher southern latitudes (McKerrow & Scotese, 1990). The map (Fig. 7) based on Ziegler (1988) shows the Cantabrian Terrane separated from Gondwana by Proto-Tethys and on its northern flank the Rheic Ocean lies between the Aquitaine Cantabrian Terrane and northern France and Britain. McKerrow & Scotese show a wedge-shaped ocean narrowing westward to the point where the Americas were in contact. Using this reconstruction, and unless there was a major climatic barrier, there would have been a possible land plant migration route between Laurussia and Gondwana. With favourable winds, airborne transport would have been feasible for many of the spores

because of their small size (Mogensen, 1981) and it is worth noting that many moss species have achieved wide dispersal in the northern hemisphere since the last ice age, some 10,000 years ago (Schofield, 1985). Such a time span is negligible in terms of geological time and is essentially instantaneous. Theoretically therefore, since there was no major physical barrier to dispersal apart from the availability of suitable habitats, and possibly climate, large parts of the tropical flora should have been uniform. As size affects dispersal (Mogensen, 1981), smaller spores, corresponding to homosporous plants with spores less than 25 µm, and appearing in the Přídolí and lowermost Lochkovian, should have had the widest distribution. Before the Pridloli, multiple unit cryptospores from the Llandovery and Wenlock, and to a lesser extent in the Upper Ordovician are apparently closely similar and widespread. Such assemblages occur in North America, Europe, North Africa, the Middle East and China. Was this wide dispersal due to efficient spore dispersal mechanisms, closer proximity of the main continents when their parent plants evolved, climate, or some other factors? The Ordovician data may not be representative, as few assemblages have been described in detail, but the uniformity of Lower Silurian cryptospore assemblages form a
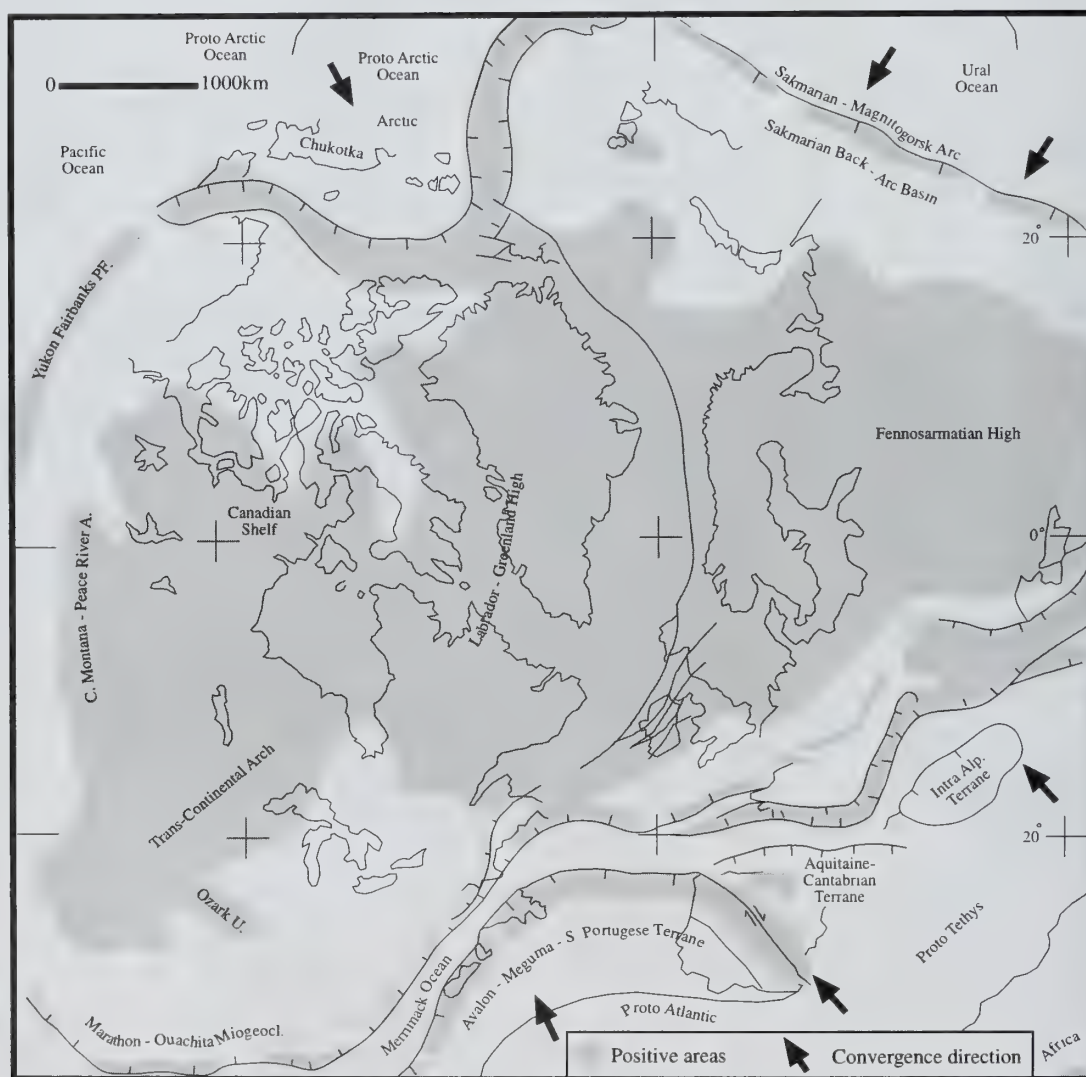


**Fig. 8**    Emsian palaeotectonic-palaeogeographic map. Simplified from Ziegler (1988).
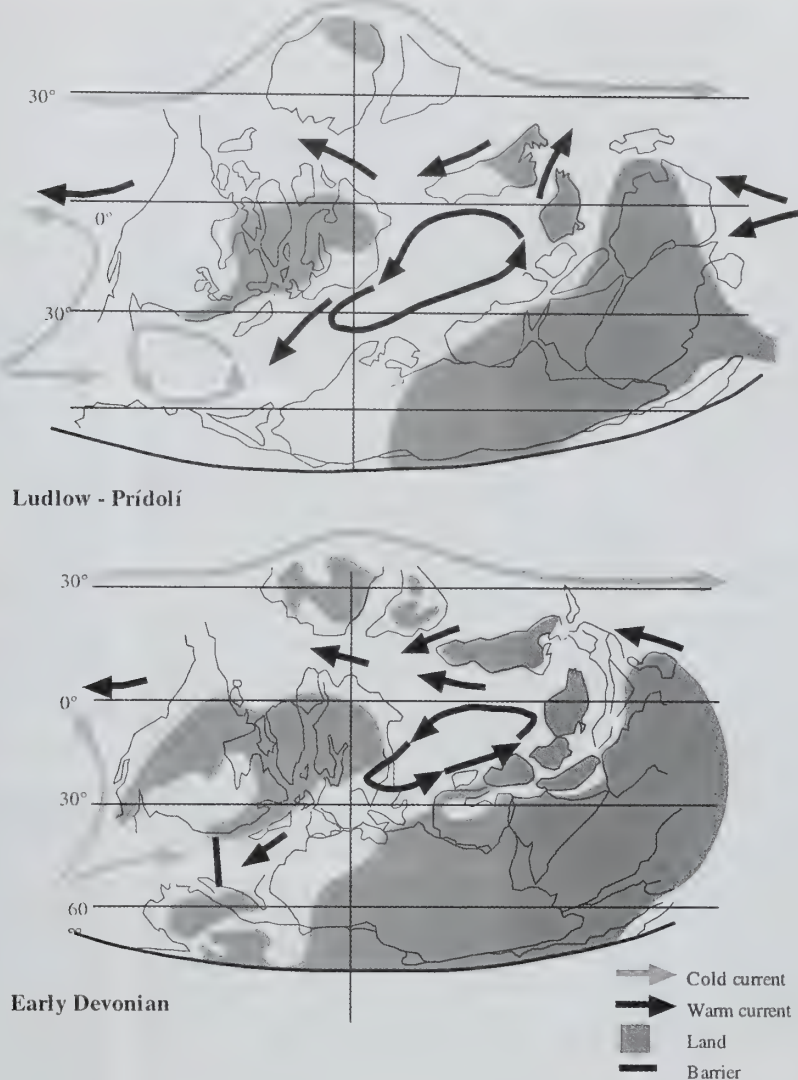
**Fig. 9** Oceanic circulation through the Ludlow-Lower Devonian. Based on Le Hérissé *et al.* (1997).

contrast to some of the Upper Silurian trilete associations showing regional variations in species distribution.

Well illustrated accounts of spore data from Upper Silurian-Lower Devonian sequences are limited to comparatively few areas, viz. Britain (Richardson & Lister, 1969), the Cantabrian Mountains (Rodriguez, 1983), and North Africa (Richardson & Ioannides 1973, and work in progress). More limited stratigraphical data are available from Belgium, France, Poland, and China. Upper Silurian and Lower Devonian spore assemblages have been described from graptolite-bearing sequences only in England and Wales (Richardson & Lister, 1969, Burgess & Richardson, 1995) and Podolia (Arkhangel'skaya, 1980). However, many of the published illustrations of the Podolian material are insufficient for detailed comparisons and key taxa cannot be identified with certainty at the species level. Nevertheless the assemblages enable general correlation of these important graptolite-bearing sequences with Britain. The following discussions are therefore based mainly upon the authors' previous and current work, and consequently the present discussion is dependent on data from a limited geographic area representing three separate blocks, namely Laurussia, Iberia-Aquitaine and northern Gondwana.

Several spore taxa (eg. *Streelispora newportensis)*, although rare in parts of Gondwana, appear to be geographically widespread. Some cryptospore taxa, eg. *Tetraletes variabilis* Cramer 1966a, may have a restricted distribution and so far have been recorded only from Gondwana, Iberia and Brittany, whereas other cryptospores (Pl. 1, figs 1, 7, 9–11) occur in Laurussia as well. The planar tetrads of *Tetraletes* occur in Silurian-Lower Devonian sections from north-west Spain and North Africa, with a single specimen recorded from Brittany (d'Erceville, 1979). It is interesting to note that similar planar tetrads are found in the modern thalloid liverwort *Riccia perssonii* from South Africa (Perold, 1989). Both the fossil *Tetraletes* and the modern *Riccia* spores are permanently adherent and are joined by more or less smooth bands of attachment separating areas of spinose sculpture. Many cryptospore taxa are found in the Silurian of North America, Britain, Western Europe, the Baltic States, Podolia, Spain, and North Africa, whereas others are apparently regionally confined. As more records are forthcoming it should be possible to
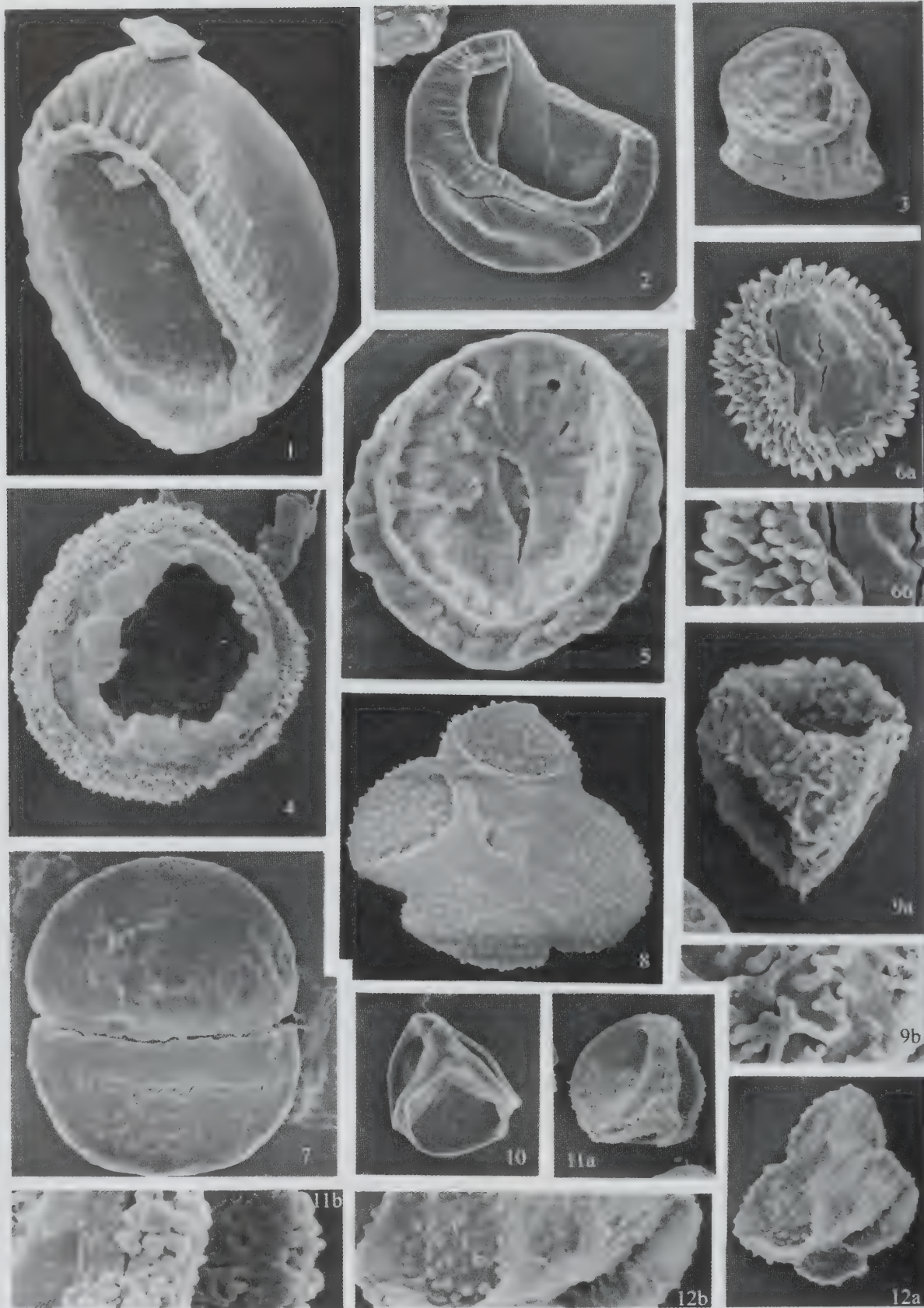
determine how many of these ubiquitous spores had evolved before the break-up of the southern continent. On the other hand, trilete species, which evolved after many of the regionally dispersed cryptospores (e.g. *Tetrahedraletes medinensis* (Strother & Traverse), Pl. 1, fig. 10), apparently show a dichotomy with several distinctive trilete species currently known only from the Cantabrian Mountains and North Africa. As more spore data accumulates, therefore, the dispersal patterns of early land floras may provide constraints to palinspastic reconstructions. In addition, new insights into the correlation of marine with non-marine plant-bearing strata, will help to date more accurately events in land plant evolution, recorded in greatest detail in continental rocks. Further, the joint study of chitinozoans and spores in the same sequences will eventually permit an understanding of inter-facies correlation, not only in marine shelf environments, but also with stratotype sequences mainly established in sediments deposited in distal marine environments where spores are often rare and badly preserved.

There is some support from the chitinozoan data for the changing regional differences in the spore data outlined above. Though the nature of sampling for chitinozoans (see below) makes any direct comparisons difficult. However, there does appear to be an increasing similarity between chitinozoan assemblages of northwest Spain and North America/Europe in the upper/later parts of all four sections studied. Due to a lack of data it is not possible to determine if there is a corresponding 'dissimilarity' with Gondwanan assemblages. Paris *et al.* (1995) noted similarities between chitinozoan assemblages in northern Spain and Gondwana and dissimilarity with coeval assemblages in Baltica during the Llandovery. This evidence was used to support the existence of a wide mid-European Rheic Ocean during the Llandovery.

Such temperal changes in our assemblages, i.e. a greater similarity with Gondwanan spore floras in the Lower Silurian, and increasing similarity with Baltic/Avalonian assemblages in the Upper Silurian/Lower Devonian, would be consistent with a drift of northwest Spain away from Gondwana and towards Laurentia/Avalonia through this period.

## CHITINOZOA

### General distribution

In sections where the Formigoso Formation is represented (Argovejo and La Vid) chitinozoans belonging to the genera *Cyathochitina* and *Conochitina* are common. The lower parts of the San Pedro Formation often contain *Angochitina* and *Sphaerochitina* with species belonging to *Plectochitina* (e.g. *Plectochitina caminae* Cramer & Diez 1978a, figs 8q, 8r and *Plectochitina rosendae* Cramer & Diez 1978a, fig. 8p) and heavily ornamented species such as *Ancyrochitina javieri* Schweineberg 1987 (figs 8f, g) becoming more common in the central parts of the formation. Certain species such as *Calpichitina velata* Wrona (1980: figs 6i, j) and *Margachitina catineria* Obut (1973: fig. 6r) occur in 'blooms' at certain horizons, for example *C. velata* at La Vid (LV6) and *M. catenaria* (Pl. 11, fig. 13) at Geras (Ger16, 17 and 18). In addition, the chitinozoans *Vinnalochitina horrentis* (Wrona, 1980), *Cingulochitina ervensis* (Paris, 1979) and *Cingulochitina serrata* (Taugourdeau & de Jekhowsky, 1960) form common components of assemblages in the San Pedro Formation (see Pl. 11, figs 8, 11a, 11b and Pl. 12, fig. 9 respectively).

### Geras (Fig. 10)

Unlike the other three sections, no Llandovery chitinozoans were recovered. *Sphaerochitina sphaerocephala* (Eisenack 1932) and *Angochitina echinata* Eisenack 1932 (Pl. 12, figs 6 and 10 respectively) were used as accompanying species in the Global Chitinozoan Biozonation of Verniers *et al.* (1995). Their presence in Ger 2b, 1.5 metres above the base of the section, suggests a mid-Gorstian to Lower Přídolí age for the lower part of the San Pedro Formation at Geras. Greater resolution is provided by *Ramochitina villosa* (Laufeld, 1974) (recovered from sample Ger 2a, 2.4 metres above the base of the section and Ger 2b; Pl. 13, fig. 7) which has been reported from the top of the Lower Leintwardine Formation and the Upper Whitcliffe Formation of the type Ludlow, UK (Sutherland 1994: 65) and from strata of similar Upper Ludfordian age on Gotland (Hamra and Sundre Beds, Laufeld, 1974: 96) and Estonia (Kuressaare Regional Stage, Nestor, 1990: 85). *Ancyrochitina valladolitana* Schweineberg 1987 (figs 8d, e) was recovered from Ger 4, 10 m above the base of the section within the San Pedro Formation. This species was described from the Palencia region of Northern Spain by Schweineberg (1987) and assigned to graptolite biozones 34/35 (Gorstian) of Elles & Wood (1901–18). However, it was noted that the chitinozoan species probably ranges into the Přídolí (Schweineberg 1987: 77).

*Ancyrochitina javieri* Schweineberg (1987: figs 8f, g) has also been recovered from Ger 4. This species was described as occurring between graptolite biozones 32 to 35 (late Homerian-Lower Gorstian) of Elles & Wood (1901–18) in the Palencia Region of Northern Spain

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**PLATE 1**

**Figs 1, 2** *Artemopyra*? sp. A. **1,** BM 137698, oblique compression showing radial folds on the proximal and distal surfaces adjacent to the curvatural ridge, × 2000, stub Ger92/9/1; **2,** BM 130612, specimen with more delicate muri than that in Fig. 1, oblique compression, × 2000, sample Ger92/8.

**Fig. 3** *Chelinohilates* sp. BM 137155, dyad showing distal and subequatorial muri, sample Geras 92/9/1.

**Fig. 4** *Cymbohilates* cf. *allenii* var. *magnus* Richardson 1996. BM 115329, proximal view showing remnants of hilum, sample Arg92/14.

**Fig. 5** *Hispanaediscus* cf. *lamontii* Wellman 1993. BM 135296, proximal view, × 2000, sample Ger92/2B/2.

**Fig. 6** *Cymbohilates* cf. *horridus* Richardson 1996. BM 130858, sample LV92/13; **6a,** proximal view; **6b,** detail of spines; × 2500.

**Fig. 7** *Hispanaediscus lamontii* Wellman 1993. BM 137471, dyad, sample Arg13/D1.

**Fig. 8** *Tetraletes variabilis* Cramer 1966a. BM 137848, tetragonal (cruciform) tetrad, sample Ger92/6.

**Fig. 9** *Velatitetras rugulata*? Burgess 1991. BM 465, LV92/6; **9a,** tetrad, lines of attachment probably covered by closely adherent envelope; **9b,** detail of geniculate disjointed muri, × 2000.

**Fig. 10** *Tetraletes medinensis* (Strother & Traverse) emend. Wellman & Richardson 1993. BM 130623, showing lines of attachment and microgranulate distal surfaces, sample Ger92/8/1.

**Fig. 11** *Pachytetras* sp. BM 138111, LV92/8/DD; **11a,** unfused tetrad showing sculpture sloughing off revealing lines of attachment; **11b,** BM 138113, detail of microverrucate-murornate sculpture, × 5000.

**Fig. 12** *Tetraletes variabilis*? Cramer 1966a. BM 132691, LV92/10; **12a,** BM 132691; **12b,** detail of microverrucate sculpture, × 2000.

All are Scanning Electron Photomicrographs at × 1000 unless otherwise stated; BM numbers refer to photographic negatives in the archives of the Natural History Museum, London.
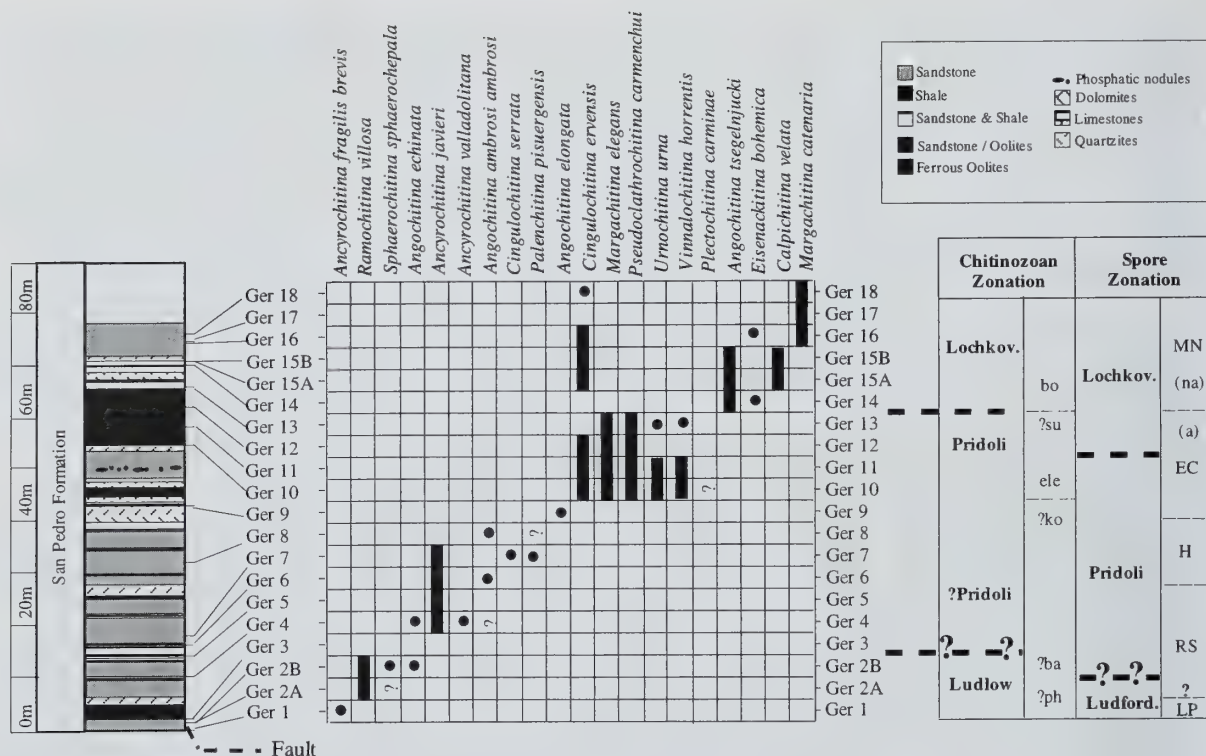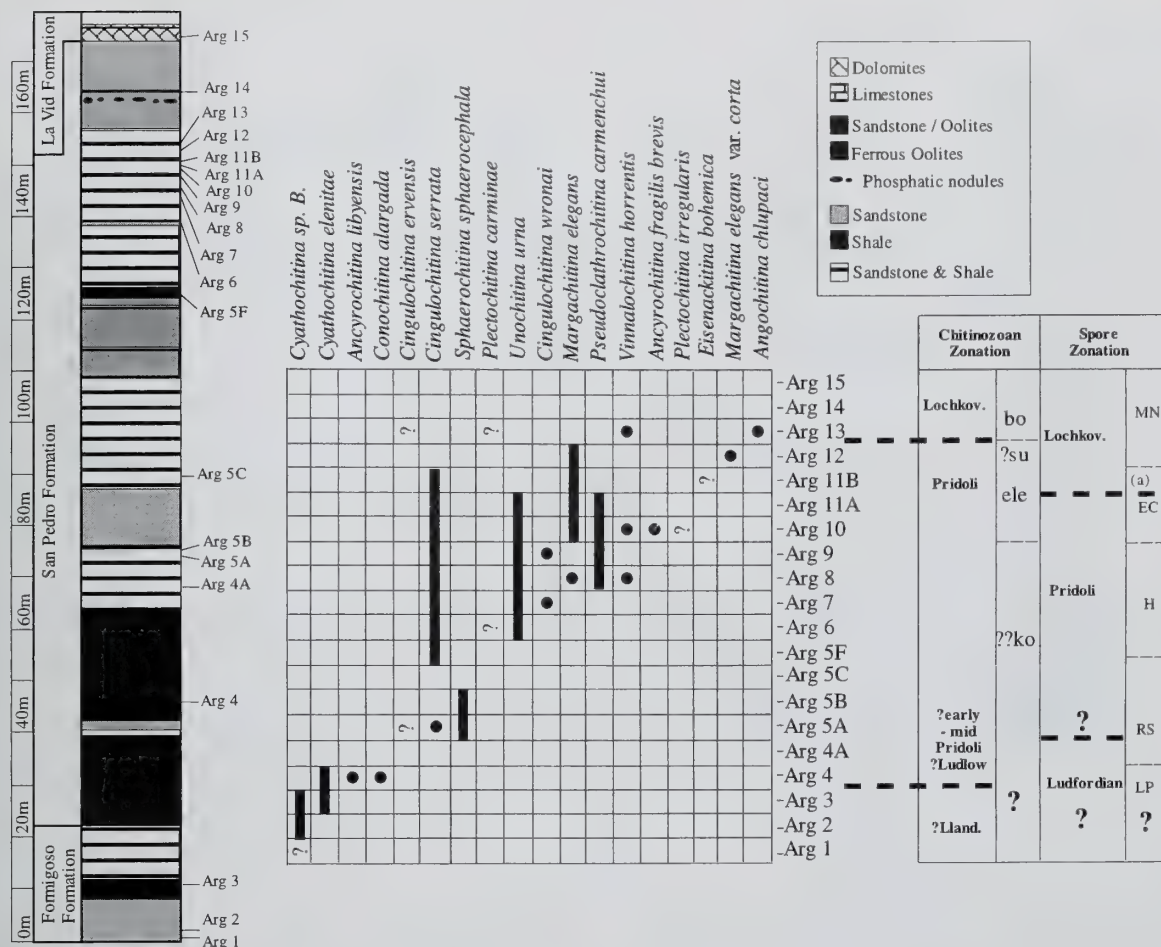
**Fig. 10**   Selected chitinozoan distribution at Geras. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi.

(Schweineberg, 1987: 70). A similar species, *Ancyrochitina* sp. A, was described by Paris from the Formation du Val in the section at Heuzé, Brittany (Paris, 1981) and is associated with *Pterochitina perivelata* Eisenack (1937), a chitinozoan with a well established range from the Upper Ludfordian to the Upper Přídolí (*barrandei* Biozone to early part of the *superba* biozone of Verniers *et al.* (1995). The presence of *Angochitina elongata* Eisenack (1931, figs 8h, i) in sample Ger 9 may be the result of reworking.

*Urnochitina urna* (Eisenack, 1934) is a very useful Přídolí marker in the stratotype area (Barandian region, Central Bohemia). *U. urna* occurs very close to (within 50 cm) or at the base of the Přídolí (although some atypical specimens do occur a few centimetres below the first occurrence of *Monograptus parultimus* (Kríz *et al.*, 1986). *U. urna* is recovered from the Geras section at Ger 10, 55 metres above the base of the section in the San Pedro Formation. In addition to *U. urna*, *Pseudoclathrochitina carmenchui* Cramer (1964b) and *Margachitina elegans* (Taugourdeau & de Jekhowsky, 1960: pl. 7, figs 92, 93) also occur in Ger 10. Both species are important markers for the mid-Přídolí *elegans* Biozone of Verniers *et al.* 1995.

In Bohemia, *Eisenackitina bohemica* (Eisenack, 1934) occurs 50cm above the base of the Devonian at Klonk, the Silurian/Devonian boundary stratotype, and Karlstejn (Paris *et al.*, 1981). At Geras, *E. bohemica* is recovered from Ger 14, 70 metres above the base of the section in the San Pedro Formation (Pl. 11, fig. 14). It is found associated with *Angochitina tsegelnjucki* Paris & Grahn (1996, fig. 7r) (Pl. 12, fig. 8). In Podolia this species is reported from the upper part of the Mitkov Formation which, on the basis of its association with *E. bohemica* and *Margachitina catenaria* Obut (1973), was assigned to the Lochkovian by Paris & Grahn (1996).

In the highest part of the section, between 74 and 76 m above the base (samples Ger 16, 17 & 18), significant numbers of a species resembling *M. catenaria* of Lochkovian age occur consistently (see p. 134). However, only a tentative assignment is made here to the Cantabrian forms as no individuals were recovered that demonstrated a convincing peduncle.

## Stage and Series Boundaries

On the basis of chitinozoans the Silurian/Devonian boundary would be placed below the first occurrence of *E. bohemica* at Ger 14. The Ludlow/Přídolí boundary is less easy to define but will occur somewhere between the first occurrence of typical Přídolí chitinozoans (*U. urna*, *P. carmenchui* and *M. elegans*) in Ger 10 but above the last occurrence of *R. villosa* in Ger 2b.

## Argovejo (Fig. 11)

An Upper Llandovery age for the Formigoso Formation at Argovejo (Argovejo 1–3; 21–10.5 metres below the base of the San Pedro Formation) is suggested by the presence of *Cyathochitina* sp. B Paris (1981: pl. 11, fig. 11) (Pl. 11, fig. 12). This species is reported from Upper Llandovery strata in the Massif Armorican by Paris (1981: 299). The discovery of the Llandovery chitinozoan *Cyathochitina elenitae* Cramer (1964b) in sample Arg 3 (Pl. 11, fig. 6) supports this age assignment. The latter species (Pl. 11, fig. 5) was also recovered with another Llandovery chitinozoan, *Conochitina alagarda* Cramer 1967 in Arg 4 (Pl. 11, fig. 2). However, as both of these species are found associated with spores from the **RS** Biozone (late Ludfordian-Lower Přídolí) they may represent reworking.

*Ancyrochitina libyensis* Jaglin (1986) was recovered from Arg 4,

**Fig. 11** Selected chitinozoan distribution at Argovejo. Chitinozoan zonation after Verniers *et al.* (1995): **bo**: bohemica, **su**: superba, **ele**: elegans, **ko**: kosovensis.

20 metres above the base of the San Pedro Formation (Pl. 13, fig. 6). Although *A. libyensis* was originally described by Jaglin (1986: 51) as a Přídolí species, Schweineberg (1987: 71) has subsequently recovered the same species from Ludlow strata of the Palencia Region of Northern Spain (Graptolite Biozones 34, 35 of Elles & Wood (1901–18), Upper Gorstian). *Sphaerochitina sphaerocephala* ((Pl. 12, fig. 6) common in the Přídolí but also ranging down into the Upper Ludlow) is recovered from Arg 5a, 52 metres above the base of the San Pedro Formation, but it is not until Arg 8, 123.5 metres above the base of the San Pedro Formation, that a typical Přídolí assemblage is encountered. Species such as *M. elegans* (associated with *Margachitina elegans* var. *corta* Cramer (1964b) in Arg 12 – Pl. 12, fig. 3), *U. urna* and *P. carmenchui* (Pl. 12, fig. 1) are common components of the assemblage. *Cingulochitina wronai* Paris & Kríz (1984) is often reported as forming an important component of Přídolí assemblages. It is recorded (Pl. 11, fig. 9) in Arg 7, 121.5m above the base of the San Pedro Formation. However, the species is also reported from the Upper Ludlow (Paris in Kríz *et al.*, 1986), Paris & Grahn (1996) and Schweineberg (1987).

Possible *E. bohemica* was recorded from Arg 11b, 128.1 metres above the base of the San Pedro Formation but a more reliable Devonian signature is provided by *Angochitina chlupaci* Paris *et. al* (1981) in Arg 13, 132.1 metres above the base of the San Pedro

Formation (Pl. 12, fig. 13). In Bohemia this species occurs within 50 cm of the base of the Lochkovian at Klonk and Karlstejn (Paris *et al.*, 1981).

## Stage and Series boundaries

The base of the Devonian is drawn below Arg 13. The base of the Přídolí is more difficult to identify but lies between Arg 4 and Arg 7 with the first occurrence of typical Přídolí chitinozoans such as *U. urna*. The base of the Ludlow will lie somewhere below the first occurrence of *S. sphaerocephala* in Arg 5a. This leaves around 57 metres of section between possible Upper Ludlow/Lower-Middle Přídolí as suggested by the recovery of *S. sphaerocephala* and the Upper Llandovery chitinozoans recovered from the Formigoso Formation in Arg 3. There are four possible explanations: 1, the Wenlock and Ludlow are very condensed in the lower part of the San Pedro Formation; 2, there is a large disconformity somewhere above Arg 3; 3, the Wenlock/Ludlow have been tectonically reduced; 4, the Llandovery chitinozoans present in the Formigoso Formation are reworked.

## La Vid (Fig. 12)

Like Argovejo, the presence of *Cyathochitina* sp. B, Paris (1981) in
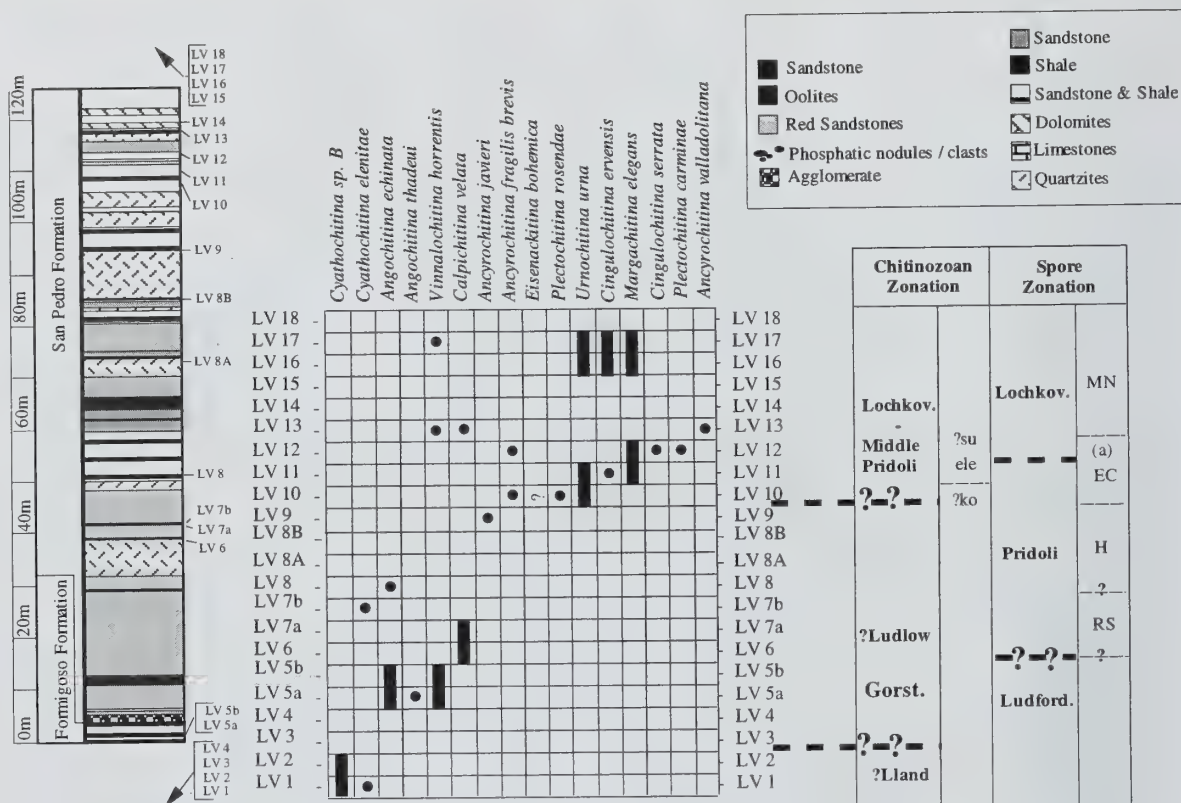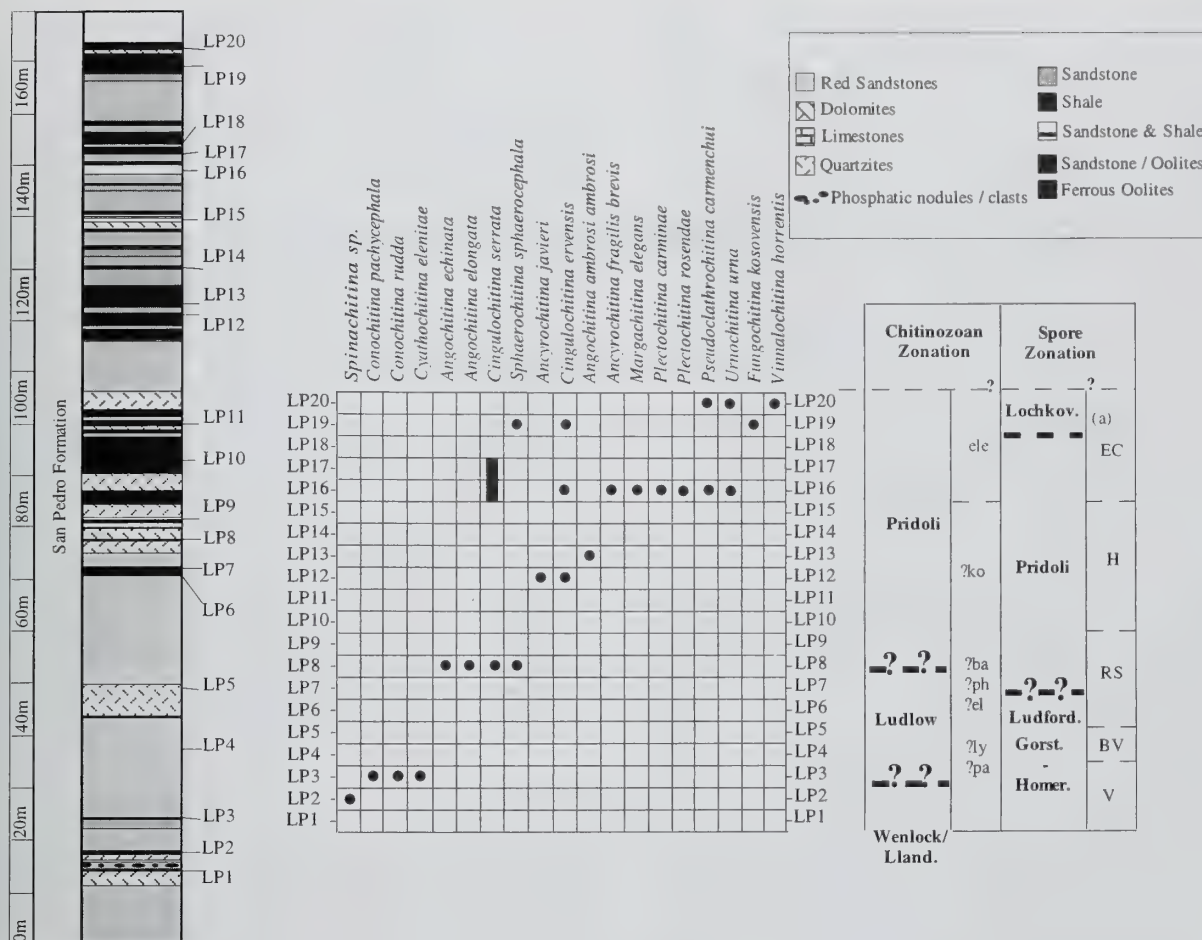
**Fig. 12**   Selected chitinozoan distribution at La Vid. Chitinozoan zonation after Verniers *et al.* (1995): **su**: superba, **ele**: elegans, **ko**: kosovensis.

LV1 and LV2 (42 m and 38.8 m below the base of the San Pedro Formation) suggests an Upper Llandovery age for the Formigoso Formation. *Angochitina echinata* Eisenack (1931) and *Angochitina thadeui* Paris (1981) (Pl. 12, fig. 11) were recovered from LV 5a. The latter has been reported from strata assigned to Graptolite Biozones 32 and 33 (Homerian to Lower Gorstian) of Elles & Wood (1901–18) by Schweineberg (1987: 59). A Llandovery age is also supported by the presence of *C. elenitae* in LV1. The recovery of this species (39 metres above the base of the San Pedro Formation at the level of sample LV 7b) is probably the result of reworking. *A. echinata* is a common species in the Middle Gorstian to Lower Přídolí (Verniers *et al.* 1995).

Typical Přídolí chitinozoans (e.g. *Urnochitina urna* – Pl. 12, fig. 4), associated with *Plectochitina* (Pl. 13, fig. 8), are not recovered until LV 10, 102.2 metres above the base of the San Pedro Formation. *Margachitina elegans* (Pl. 12, fig. 5), used as an index species for the mid-Přídolí by Verniers *et al.* (1995), is first encountered in LV11, 107.8 m above the base of the San Pedro Formation. *Ancyrochitina fragilis brevis* Taugourdeau & de Jekhowsky (1960) was recovered from LV10 (Pl. 13, fig. 5). This species was regarded as a 'late Ludlow' species by Cramer & Diez (1978a). Samples LV 10, 11, and 12 are regarded as lowermost Devonian based on the spores but no chitinozoans were recovered that could be positively identified as Devonian. The spores in sample LV 13, *c.* 1 m above LV 12, are typical of the lower **MN** Biozone (**NA** Subzone) of Lower Lockhovian age.

### Stage and Series boundaries

No Devonian chitinozoans were recovered from La Vid and typical Přídolí forms such as *Pseudoclathrochitina carmenchui* and *M.*

*elegans* were still recovered from the top of the section. However, the first appearance of *Aneurospora* is used tentatively to place the base of the Devonian below LV10 (see also Richardson, Rodriguez & Sutherland, 2000). The base of the Přídolí is placed somewhere below LV10 with the first occurrence of *U. urna*. As with Argovejo, the presence of Upper Llandovery chitinozoans in the Formigoso Formation may suggest the presence of a disconformity or the reworking of Lower Silurian faunas. The spacing of some samples, because of unsuitable lithology and poor recovery from others, makes a more precise biostratigraphy difficult at this time.

### La Peral (Fig. 13)

Because *Spinachitina* has not been reported above the Llandovery, the presence of *Spinachitina* sp. in LP2 (Pl. 11, fig. 4) 18 meters above the base of the San Pedro Formation may suggest either a pre-Wenlock age for this part of the section or possibly evidence for reworking. *Conochitina rudda* Sutherland (1994), present in LP3, 24.6 metres above the base of section, has been described from the Upper Wenlock/Lower Ludlow of the type area in the Welsh Borderlands (Sutherland, 1994: 48). *Conochitina pachycephala* Eisenack 1964, present in LP3 (Pl. 11, fig. 1), is used as an index species for the mid-Upper Wenlock but also ranges well into the Gorstian (Verniers *et al.* 1995). The presence of *Cyathochitina elenitae* (Pl. 11, fig. 3) in the same sample may be the result of reworking. The recovery of *Angochitina echinata* (Pl. 12, fig. 10) suggests an age of at least Middle Gorstian to Lower Přídolí (Verniers *et al.,* 1995) for LP 8, 77.5 m above the base of section. *A. elongata*, recovered from the same sample, was used as a mid-Ludlow zonal indicator in the biozonation of

**Fig. 13** Selected chitinozoan distribution at La Peral. Chitinozoan zonation after Verniers *et al.* (1995): **ele**: elegans, **ko**: kosovensis, **ba**: barrandei, **ph**: philipi, **el**: elongata, **ly**: lycoperdoides, **pa**: pachycephala.

Verniers *et al.* (1995). Not until LP16, 149.5 metres above base of section, is a Přídolí chitinozoan assemblage containing *U. urna, M. elegans* and *P. carmenchui*, recovered. *Fungochitina kosovensis* Paris & Kríz (1984), is found in LP19, 169 meters above the base of the section (Pl. 12, fig. 7) but is more commonly described from the Lower- mid-Přídolí (Paris & Kríz, 1984, Verniers *et al.*, 1995). The uppermost sample LP 20 at La Peral contains *Urnachitina urna* (Pl. 11, fig. 10) associated with *Pseudoclathrochitina carmenchui* (Pl. 12, fig. 2). As with La Vid, chitinozoan evidence for a Přídolí age contradicts the interpretation based on spore data, which places the base of the Lochkovian between LP 18 and 19 from the presence of *Aneurospora* in LP 19.

### Stage and Series boundaries

It is not possible to suggest a base for the Devonian on the basis of the chitinozoans recovered from this section. The base of the Přídolí is tentatively placed somewhere below LP 16 (although it must be noted that *A. echinata*, present in LP 8, can also be recovered from the Přídolí). As with La Vid, additional sampling should increase the resolution of chitinozoan biostratigraphy in this section.

## COMPARISON OF THE CHITINOZOANS FROM THE CANTABRIAN MOUNTAINS WITH COEVAL SECTIONS AND THE GLOBAL BIOZONATION SCHEME

Direct statistical comparisons are not made here as samples were not prepared specifically for Chitinozoa and the rarest forms may have been overlooked or destroyed. However, it is possible to make general comparisons with coeval sections.

### Palencia Province, northern Spain

Palencia is located in the Cantabrian Mountains to the east of our sections in Northern Spain and demonstrates many similarities in chitinozoan assemblages. Schweineberg (1987) noted the presence of *Cyathochitina* spp. in the Las Arroyacas Formation (possibly equivalent to the Formigoso and the lower part of the San Pedro Formations) in Palencia, which he regarded on the basis of graptolites as Wenlock (*lundgreni* Biozone). In our material we find *C. elenitae* in the lower part of the San Pedro Formation. Firstly in the **V** Biozone (Homerian to Lower Gorstian,

La Peral) and secondly an occurrence in the **RS** Biozone (Upper Ludfordian to Lower Přídolí). This suggests some reworking in our sections. *U. urna* forms an important part of assemblages in both regions and is considered by Schweineberg (1987) to be restricted to the Přídolí in Palencia. See preceding discussion of our sections and further discussion of the Asturias-León/Palencian chitinozoan ranges below. The two regions share the following Ludlow/Přídolí species: *Ancyrochitina javieri, Angochitina echinata, Angochitina elongata, Angochitina thadeui, Conochitina pachycephala, Cyathochitina elenitae, Margachitina elegans* var. *corta, Ancyrochitina libyensis, Ancyrochitina valladolitana, Angochitina ambrosi ambrosi, Cingulochitina wronai, Palenchitina pisuergensis, Plectochitina carminae;* Cantabrian specimens are figured in Pl. 12, figs 3, 12, 14, Pl. 13, figs 1–4, 9.

## Prague Basin (Bohemia)

The Prague Basin is both the type area for the base of the Přídolí (Pozary, 1km east of Reporyje) and the base of the Devonian (Klonk, SW of Prague). The characteristic chitinozoan of the Upper Ludlow, *Eisenackitina barrandei* Paris & Kríz (1984), was not recovered from our sections. Only species that extend into the Přídolí in Bohemia were recovered in the Cantabrian Mountains (*S. sphaerocephala, C. wronai*). *U. urna* is a common component of assemblages in the middle to upper portions of the San Pedro Formation. It is regarded as a useful Přídolí marker (see Paris *in* Kríz *et al.*, 1986) although atypical forms do occur 'a few cm' (Paris in Kríz *et al.*, 1986: 338) below the first occurrence of *Monograptus parultimus.* The only other chitinozoan regarded as an Lower Přídolí form in Bohemia, *F. kosovensis,* is recorded towards the top of the section at La Peral (LP19). In Bohemia the base of the Devonian is regarded as being coincident or very close to the first occurrence of *E. bohemica. A. chlupaci* is also regarded as a Lower Lochkovian form (Paris *et al.*, 1981). Both these species occur in the Cantabrian Mountains and are associated with Devonian spores (see description of chitinozoan distribution in Geras and Argovejo). As in Bohemia, *C. velata* (chitinozoan indet. n. gen? in Paris *et al.*, 1981) occurs close to the top of the Silurian in the Cantabrian Mountains (Pl. 11, fig. 7).

## The Type Ludlow Sections

Sutherland (1994) described chitinozoans from the type Ludlow in the Welsh Borderlands of the UK. The Lower Ludlow in the type area is characterized by *Conochitina* Eisenack (1931) species and in particular *C. rudda* and *C. pachycephala.* Both these species are recognized in our sections, but only from one sample at La Peral (LP3) in the San Pedro Formation. *Angochitina echinata* is a common component of mid-Ludlow assemblages in the Welsh Borderlands and occurs sporadically through the San Pedro Formation. In the Ludfordian, *R. villosa* is the only species we find in common with the type area where this species is a useful marker for the mid- to upper Ludfordian. Due to poor chitinozoan recovery from the latest Ludlow and Lower Přídolí in the Welsh Borderlands (probably as a result of an increasing fresh water influence) any further comparisons are difficult.

## Podolia, Ukraine

A provisional study of Silurian and Devonian sections of this area was detailed in Paris & Grahn (1996). Six assemblages were defined, the age controlled with reference to chitinozoan index taxa in Bohemia (Kríz *et al.*, 1986; Paris *et al.*, 1981). Assemblage 1 from Podolia, characterized by *E. barrandei* was not encountered

in our study. Podolian chitinozoan assemblage 2 containing *U. urna, M. elegans* and *F. kosovensis* was regarded as Lower to mid-Přídolí in age. The same species are encountered in our study within the San Pedro Formation. The characteristic chitinozoan of Paris & Grahn's assemblage 3 (Upper Přídolí), *C. velata,* was recovered from the San Pedro Formation at La Vid and Geras. Paris & Grahn (1996) take the base of the Devonian in Podolia as being coincident with the base of the Podolian chitinozoan assemblage 4. The zone is defined by the first occurrence of *E. bohemica,* which is also associated with *M. catenaria.* Both these species (although *M. catenaria* somewhat dubiously in Geras) are present in the upper parts of the San Pedro Formation. *A. tsegulnjucki,* regarded as a characteristic species of Paris & Grahn's assemblage 5 (Lochkovian) coincides with the range of *E. bohemica* in Geras. It is important to note that Paris & Grahn's location of the Silurian/Devonian in Podolia is in disagreement with the assignment of previous workers who have placed the boundary at the first occurrence of *Monograptus uniformis angustidens* (e.g., Koren' 1968). The base of the Devonian at the type section at Klonk coincides with the first occurrence of *Monograptus uniformis uniformis* (Holland, 1985), a closely related subspecies. At Klonk both graptolites occur at the same level but in Podolia the first *Monograptus. u. uniformis* occurs higher than *Monograptus u. angustidens.* As *E. bohemica* occurs very close to the first appearance of *Monograptus u.uniformis* in both sections, Paris & Grahn (1996) elected to draw the Silurian/Devonian boundary at the base of the range of *E. bohemica* and *Monograptus u. uniformis.*

## Eastern Canada

Achab & Asselin (1993) describe *Cingulochitina ervensis, C. serrata* and *Urnochitina urna* from the Chaleurs Group in the northeastern Gaspé Peninsula. These species form common components of assemblages in the San Pedro Formation. Achab & Asselin used the presence of *E. bohemica, M. catenaria* and *A. chlupaci* to define the base of the Devonian in this area of Canada. In the Cantabrian Mountains, the same species are found associated with or at a level above the first occurrence of *Aneurospora,* taken by Richardson, Rodriguez & Sutherland (2000) to represent the base of the Devonian.

## North Africa

Taugourdeau & Jekhowsky (1960) published data from core material from the Sahara. It is difficult to compare the material from our area with that of North Africa with any great certainty, due to the relative lack of stratigraphical control and difficulty in positively identifying chitinozoans from the silhouettes presented in the plates of the paper. However, *C. serrata. M. elegans* and *E. bohemica* are recorded by Taugourdeau & Jekhowsky (1960) in a broad zone defined as 'Gothlandian' (approximately equivalent to the Silurian) to Lower/Middle Devonian.

Jaglin (1986) examined core material from the Upper Silurian (mostly Přídolí) of Libya. Jaglin made age determinations based on well-known Přídolí chitinozoans such as *U. urna, P. perivelata, M. elegans* and *P. carmenchui.* Many of the species recorded from the Přídolí by Jaglin (1986) were also encountered in the Cantabrian Mountains. These include: *A. libyensis, V. horrentis, C. serrata, F. kosovensis, R. villosa, M. elegans, P. carminae, P. carmenchui, S. sphaerocephala* and *U. urna.* Of these, only the ranges of *A. libyensis* and *V. horrentis* were detailed by Jaglin, all of which were shown as being present close to the base of the Přídolí in borehole A1–61.

## SILURIAN GLOBAL CHITINOZOAN BIOZONATION

The global scheme of Verniers *et al.* (1995) was calibrated with reference to chitinozoan index species in global stratotype sections and other localities, or by reference to graptolite, conodont or trilobite biozonal schemes where this information was not available. To be included in the scheme, index species had to have been recorded from at least two major Silurian palaeocontinents.

*Conochitina pachycephala* was used as the index species for the Middle-Upper Wenlock *pachycephala* Biozone. This species was recovered in our study from one sample close to the base of section at La Peral (LP3). As *C. pachycephala* ranges well into the Gorstian and because the succeeding Upper Homerian *lycoperdoides* Biozone was not encountered, it is not possible to increase the resolution of this part of the San Pedro Formation with chitinozoan data.

*Angochitina elongata* was used as the index species for the Middle Ludlow biozone in the global scheme but was only recorded sporadically from La Peral and Geras. At Geras (Ger 9) it is possible that the species is reworked as it is found associated with spores attributed to the lower **EC** Biozone, which is regarded as Upper Přídolí in age. At La Peral, *A. elongata* occurs in sample LP8 and is associated with spores attributed to the Ludlow **RS** Biozone. *A. echinata* is noted as an accompanying species in the *elongata* biozone of the global scheme and was recovered from La Peral, La Vid and questionably from Geras. Although a common component of many Middle and Upper Ludlow chitinozoan assemblages it is known to range into the Lower Přídolí (Verniers *et al.* 1995).

No chitinozoans were recovered from the Cantabrian Mountains that could be directly attributed to the Middle Ludfordian *philipi* Biozone or the Upper Ludfordian *barrandei* Biozone of the global scheme. *S. sphaerocephala*, recovered from Geras, La Peral and Argovejo, is shown to range through the *barrandei* Biozone by Verniers *et al.* (1995), but is also noted as ranging into the Middle Přídolí.

The Lower Přídolí *kosovensis* biozone is well represented in most areas globally by the presence of *U. urna*, which was recovered from all four sections studied. The index species *Fungochitina kosovensis* is recorded from La Peral, but in only one sample (LP 19) at a level well above the base of the following *elegans* Biozone.

The *elegans* Biozone is well represented in our sections by the index species, *Margachitina elegans,* in all sections, often associated with *P. carmenchui* and *U. urna*.

The index taxa for the Upper Přídolí *superba* Biozone (*Anthochitina superba* Eisenack, 1971) has not been recorded in this study, with only the accompanying species *U. urna* encountered. The top of the *superba* Biozone and the base if the first biozone in the Devonian is defined by the first occurrence of *E. bohemica*, regarded as being coincident with the base of the Devonian (Paris, Winchester-Seeto & Grahn, 2000) *E. bohemica* has been identified from Geras in samples Ger 14 and 16.

## BIOSTRATIGRAPHICAL CONCLUSIONS

The **vetustus** (**V**) and **brevicosta – verrucatus** (**BV**) Spore Biozones indicate an age no earlier than Homerian. Chitinozoan evidence is sparse but the range of *Conochitina rudda* in sample LP3 includes the Upper Homerian. There is thus a possible disconformity between the **BV** spore assemblage ( Upper Homerian) in the La Peral section and the **reticulata – sanpetrensis** (**RS**) assemblage (Ludfordian to Lower Přídolí). The base of the **RS** Biozone is not seen in the sections studied with the possible exception of La Peral.

### Ludfordian/Přídolí boundary

Because of differences in chitinozoan assemblages between the Cantabrian Mountains and the type area in Bohemia, and possibly sampling deficiencies due to the coarseness of some of the sediments, it is currently not possible to define this boundary with precision. However, the occurrence of several forms, such as *Ramochitina villosa* at Geras, indicate a Upper Ludfordian age, consistent with spore evidence that places the boundary in the **RS** Biozone. Spore assemblages from the Welsh Borderland show many species in common with those from Spain, but the lower Cantabrian samples (Formigoso and the lower part of the San Pedro Formation) often yield poor results and the key forms from the Anglo-Welsh area are usually missing or have a sporadic distribution. Consequently, the exact level of the lower **RS** boundary is uncertain. The approximately equivalent **LP/TS** (Ludfordian/ Přídolí) boundary in the type area has not been located but the spore assemblages below the **RS** Biozone have some comparable features to the lower **LP** Biozone (mid- Gorstian to Ludfordian) and spores similar to the nominal species of the *Chelinospora obscura* Sub-Biozone (mid-Gorstian) and the overlying *cambrensis* and *inframurinatus* Sub-Biozones occur in the **RS** Biozone. Few other independently dated sections have been studied palynologically across the Ludfordian/Přídolí boundary elsewhere, so the location of the lower boundary of the Přídolí Stage must remain provisional.

### Silurian/Devonian boundary

In the Silurian/Devonian boundary stratotype (Klonk section, Bohemia), *Eisenackitina bohemica* and *Angochitina chlupaci* appear close to the base of the Devonian. They are also found in the Geras and Argovejo sections respectively, where the base of the Devonian (based on spore data – Richardson, Rodriguez & Sutherland, 2000) is also a little lower than the appearance of these two chitinozoan species, and close to the base of the *Aneurospora* spp. Sub-Biozone. This latter assemblage is found in three of the four Cantabrian sections studied, and occurs also in the Anglo-Welsh area above the thelodont *Turinia pagei* at a level 30 m below the base of the **MN** Biozone. The **MN** Biozone occurs near the base of the Gedinnian in Belgium and above the basal Devonian graptolites in Podolia (Ukraine). Consequently, although further work needs to be done on sections (e.g. Podolia) containing spores, chitinozoa, and key macrofossils, the *Aneurospora* spp. Sub-Biozone has potential for inter-regional correlation, and its base, on current evidence, including chitinozoan work in this paper, is near, if not coincident with, the Silurian/Devonian Boundary.

### Radiometric dates and Přídolí basal Devonian timescales

Recently construed radiometric dates (Tucker *et al.,* 1998) give ages for the Upper Ludfordian (Whitcliffe) and basal Devonian (Lochkovian) as $420 \pm 4$ Ma and $417.6 \pm 1$ Ma respectively. This leaves a minimum of 2.4 Ma for the duration of the Přídolí. Our researches on sequences from the Cantabrian Mountains indicate one spore zone in this interval with parts of two others. Previously, Richardson *et al.* (1984) estimated duration of *c.* 3 Ma for each spore zone. Using roughly 1 2/3 zones this would give a figure of approximately 5 Ma for the duration of the Přídolí Stage. This seems more realistic for the biological changes involved. The maximum interval (7.4 Ma) indicated by the radiometric dates would allow for at least 2.5 biozones of average duration.

## MATERIALS AND METHODS

Type and figured palynomorphs for this paper are housed in the Palynology Laboratory, Department of Palaeontology, The Natural History Museum, London. Figured specimens have either FM numbers (spores) or FC numbers (chitinozoa). Spores are located on slides, while for SEM images the number refers to the relevant stub. Letters and numbers (eg. LV 92/17 (DE) 3, 179 0914) refer to section, year of collection, sample, (maceration), slide number and lastly the specimen location co-ordinates taken on a Zeiss Photomicroscope III (n. 2562) housed in the Palynology Section of the Palaeontology Department. E.F. numbers are the England Finder co-ordinates (e.g. J33/1) of the specimen location. BM numbers refer to SEM photographic negatives held in the archives of The Natural History Museum, London. SEM stubs and strew, or picked specimens, were coated with gold palladium. Spores were studied on Hitachi S800 and Phillips XL 30 field emission SEM's and, in addition, some chitinozoans were studied on a Hitachi S2500. Mounting methods for the chitinozoa are as described by Sutherland (1994); spores are strewn, mainly on mica, secured to the stub with araldite S2. Numbering of chitinozoan specimens follows the same pattern as described for the spores, eg. sample number ARG11A, slide number 508/12, stub box reference SB4/45, England Finder reference (Q27/4).

The light photomicrographs were taken on a Zeiss photomicroscope using Normarski differential interference with × 60 or × 100 objectives and a plate camera and were all taken by Mr. Peter York of the Natural History Museum.

Sporomorphs and chitinozoa were extracted from rock samples using standard palynological methods. Because of the high maturation of much of the material schultze's solution was usually used but light microscope and SEM studies revealed that even very fine sculptural detail was preserved, comparable with that seen in English Lower Devonian material with low maturation (Richardson, 1996b). Residues were strewn on slides and dried and covered with either elvacite or epoxy resin.

A duplicate set of samples is preserved in the Mining and Engineering Department, University of León.

## TAXONOMY OF SELECTED SPORE TAXA

Anteturma **SPORITES** H. Potonié 1893
Turma **TRILETES** (Reinsch 1881) Potonié & Kremp 1954
Subturma **AZONOTRILETES** Luber 1935
Genus ***RETUSOTRILETES*** (Naumova) Richardson 1965

TYPE SPECIES.    *Retusotriletes pychovii* Naumova 1953 (lectotype species of Richardson 1965).

REMARKS.    The great variability of smooth taxa is illustrated by Rodríguez (1983). Two genera in particular show a great deal of variation. The genus *Archaicusporites* has a thin proximal face with an apical triangular thickening, but otherwise is similar in structure to the genus *Archaeozonotriletes*. There is also a complex of retusoid spores and, in particular, the spores placed in the species *R. coronadus* Rodríguez 1983 include laevigate forms, and forms with apiculate sculpture which herein are placed in two genera.

***Retusotriletes bipellis*** Rodriguez, 1978                    Pl. 2, fig. 1

Rodriguez, 1978c: pl. 3, fig. 2; San Pedro Formation, Torrestio, Province of León, Cantabrian Mountains, northwest Spain.

DIMENSIONS.    Rodriguez 1978c, 40–70 μm; present study 30–48 μm (based on 10 specimens).

REMARKS.    These miospores have a thin proximal exine and may grade into species of *Archaicusporites*.

OCCURRENCE.    Found in all sections, occurring from the **EC** Biozone to the **NA** Sub-Biozone (**MN** Biozone), Upper Přídolí and Lower Lochkovian.

***Retusotriletes coronadus*** (Rodriguez, 1983) emend

1978    *Retusotriletes communis* Naumova; Rodriguez: pl. 4, fig. 12.

1983    *Retusotriletes coronadus* Rodriguez (pars): pl. 9, figs 1, 10? (non pl. 8, figs 1, 8).

DIAGNOSIS.    Trilete retusoid azonate spores with relatively thin contact areas and a thickened proximal triangle surrounding a thin apical area.

COMPARISONS.    *Archaicusporites asturicus* and *A. torrestionensis* (Rodriguez, 1983) (Pl. 10, fig. 8) are similar but have thicker equatorial and distal walls.

REMARKS.    Spores originally placed in this taxon show considerable morphological diversity. The figure of the holotype (Rodriguez, 1983: pl. 9, fig. 1) is different from the other specimens illustrating the original description, and appears to have a dark triangle on the proximal surface similar to *Archaicusporites asturicus* (Rodriguez, 1983: pl. 7, fig. 3). The epithet *R. coronadus* is retained pending re-examination of the holotype. Other spores belong to two separate morphologies, the first (Form 1) with a highly distinctive double curvaturate structure (Rodriguez, 1983: pl. 8, fig. 1), the second

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**PLATE 2**

**Fig. 1** *Retusotriletes bipellis* Rodriguez 1978c, FM 1496. **1a,** shows Y-mark and folded proximal membrane; **1b,** double ridged curvaturae and laevigate distal exine, Ger92/15a, (469) 3, 213 0959.

**Figs 2, 3** *Retusotriletes? saturnus* sp. nov. **2a,** FM 1498, proximal view shows distinct triangular area at the spore apex; **2b,** shows concentric curvatural thickenings, LV92/17 (D3) 3, 152 0928; **3,** FM 1497, proximal view showing trilete folds, LV92/17 (D3) 3, 179 0914.

**Fig. 4** *Apiculiretusispora arcidecus* sp. nov. FM 1499. **4a, 4b,** proximal view, showing grana and microconi forming the curvaturae perfectae; **4c,** detail of curvaturae at radial apex, × 1,500, LV92/13 (D3) 1, 066 0952.

**Figs 5–7** *Breconisporites?* spp. **5,** FM 1500, proximal view with an equatorial crassitude, arcuate zones of thickening, thinnest in the radial areas surrounding a thin apical triangular area with radial folds, and a distal polar thickening, Arg92/14 (468) 11, 138 0893; **6,** FM 1501, similar specimen with distinctly granulate equator, LV92/13 (495) 2, 195 0960; **7a, b,** FM 1502; **7a** proximal view; **7b** distal focus showing annulus and polar thickening, slide Arg92/14 (468) 11, 083 1072.

**Fig. 8** *Emphanisporites splendens* Richardson & Ioannides 1979. **8a, 8b** FM 1503, showing radial ribs, distinct annulus and large inter-radial thickenings, Ger92/2B (477) 2, 165 0961.

**Fig. 9** *Emphanisporites* sp. FM 1504, Ger92/2B (477) 2, 166 0898.

All figs × 1000, unless stated otherwise.
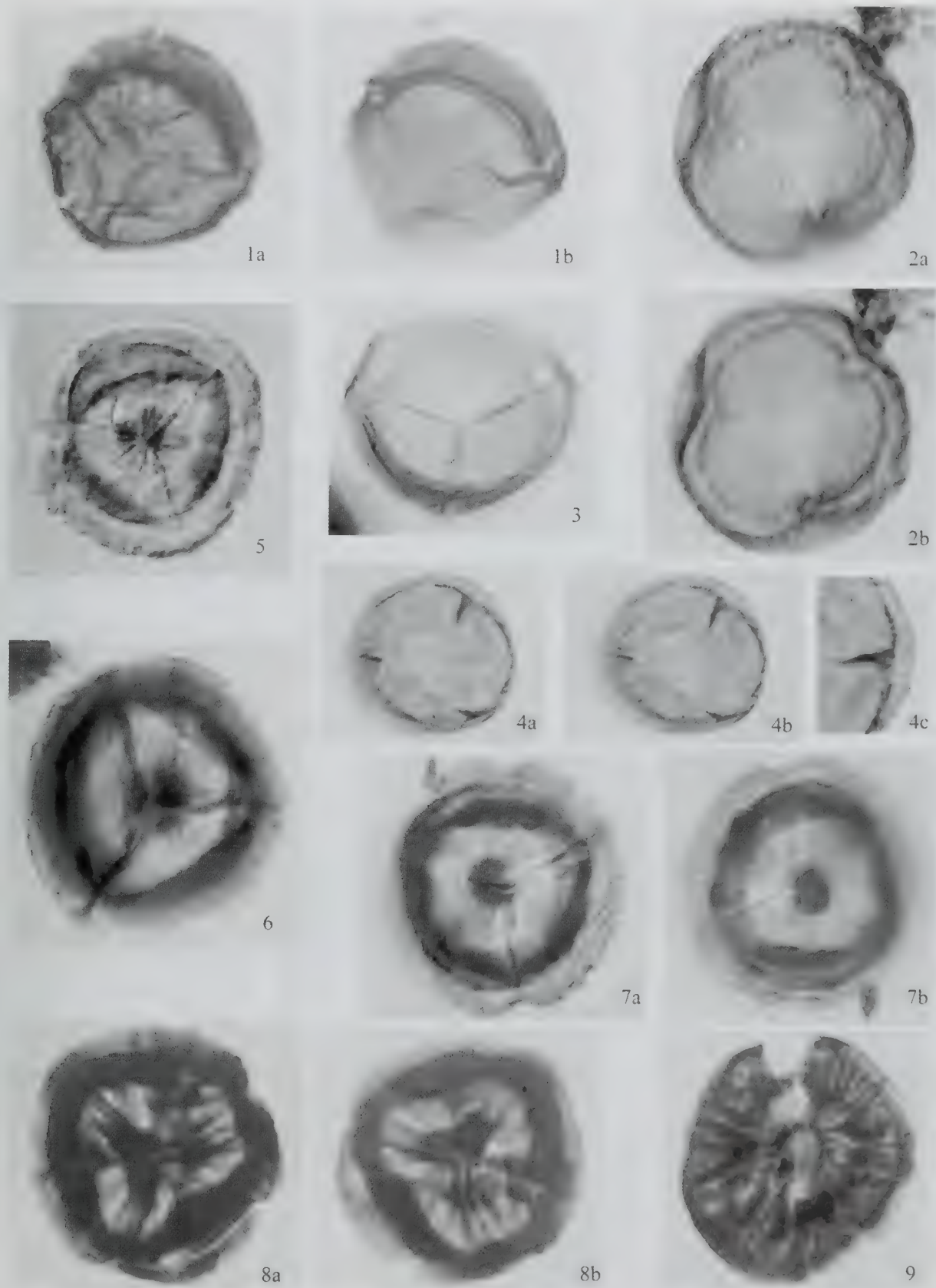
(Form 2) with curvaturae formed from bands of sculpture (Rodríguez, 1983: pl. 8, fig. 8). In England the spores with arcuate lines of sculpture (curvaturae) show a morphological sequence of increasing complexity through the Přídolí and into the Lochkovian. The same trend to a lesser extent is seen in spore assemblages from the Cantabrian Mountains. Two azonate species are illustrated in Rodriguez (1983). Form 3 is zonate and new but the curvaturate sculptural pattern is similar to that seen in Form 2. The three forms are referred to in the text as follows.

Form 1: *Retusotriletes*? *saturnus* sp. nov.

Form 2: *Apiculiretusispora arcidecus* sp. nov.

Form 3: *Breconisporites*? spp. (cf. *Retusotriletes coronadus* Rodriguez).

## *Retusotriletes*? *saturnus* sp. nov. Pl. 2, figs 2, 3; Pl. 3, fig. 1

1983    *Retusotriletes coronadus* Rodriguez: 46: pl. 8, fig. 1 only.

DERIVATION OF NAME.    Latin m. Saturnus, Saturn, referring to the concentric rings, i.e. double curvaturae surrounding the spore.

HOLOTYPE.    Rodriguez, 1983: figs 3, 43, pl. 8, fig. 1.

DIAGNOSIS.    Distally laevigate retusoid trilete spores with two curvaturate bands; the inner band forms a raised wedge-shaped band and joins with the trilete folds.

DESCRIPTION.    Amb +/– circular, hemispherical in lateral view with more flattened proximal surface. Exine distally laevigate and proximally microrugulate to scabrate; rugulae often more pronounced between the two curvaturate bands, inner band *c.* 5/8 spore radius, slightly invaginated at the radial apices, outer band +/– equals spore radius, although often markedly invaginated radially. Curvaturate bands distinct, equatorial margin of inner curvaturae minutely ir-regular, outer curvaturate band with smoother margin, forming a distinct narrow extension, trilete rays with slightly sinuous low lips.

DIMENSIONS.    30–49µm (16 specimens measured).

COMPARISONS.    The double curvaturate band and distinctive proxi-mal microsculpture distinguish these spores from other species of the genera *Retusotriletes* and *Scylaspora*. *R. bipellis* does not have the scalloped inner 'curvaturae' and the proximal surface appears to be smooth. The type material was not available for comparison.

OCCURRENCE.    Upper San Pedro Formation, upper **EC** and lower **MN** Sub-Biozones, Argovejo; upper **EC** (*Aneurospora* Sub-Biozone) Geras; uppermost **EC** (*Aneurospora* Sub-Biozone), La Peral; and lower **MN** Sub-Biozone La Vid; uppermost Přídolí and Lower Lochkovian.

REMARKS.    *Retusotriletes*? *saturnus* sp. nov. forms part of the original *R. 'coronadus'* complex of Rodriguez (1983) and occurs in the highest Přídolí and Lower Lochkovian in the Cantabrian Moun-tains. So far this species has not been found in the Anglo-Welsh area, where few sections of this interval have produced spores. The proximal surface of *R. saturnus* is quite distinctive. The inner curvaturae form a wedge-shaped thickening and invaginate at the contact with the often indistinct trilete folds. The proximal surface is scabrate to microrugulate (under SEM), a feature that is specially marked between the inner and outer curvaturate zones. The outer curvaturae are coincident with the equator except in the inter-radial areas and the distal surface is smooth. In equatorial view, under the SEM, the spore resembles a limpet, with the raised inner curvatura resembling a mantle, and the outer curvatura resembling the shell. The structure of *R. 'coronadus'* however, with its wedge-shaped inner curvatural band, revealed by SEM studies, is distinct both from the species holotype figured by Rodriguez (1983: pl. 9, fig.1) and from *A. archidecus.*

## Genus *APICULIRETUSISPORA* Streel, 1964

## *Apiculiretusispora arcidecus* sp.nov                    Pl. 2, fig. 4

BASIONYM.    *Retusotriletes coronadus* Rodriguez, 1983 (*pars*) .

1983    *Retusotriletes coronadus* Rodriguez (*pars*); Rodriguez: 46, pl. 8, fig. 8.

DERIVATION OF NAME.    Latin *arc*, arch or arc, *decus*, ornament; referring to the curvatural sculptured zones.

HOLOTYPE.    Rodriguez, 1983: pl. 8, fig. 8.

DIAGNOSIS.    Retusoid spores with scupture of grana and coni con-fined to the curvaturae and borders of the trilete mark.

DESCRIPTION.    Amb circular to sub circular, trilete mark distinct, laesurae labrate, 4/5ths radius, sculptural elements form the curvaturae perfectae, may connect with broad bands of sculpture which border the lips, and can also occur on the lips. Sculptural elements variable from barely discernible to distinct under the light microscope; elements consist of micrograna, microconi and coni, >1–1.5µm high and wide. Proximal equatorial areas, outside the contact areas, and distal surface laevigate.

DIMENSIONS.    28–43 µm.

COMPARISONS.    This species is distinguished by curvaturae

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**PLATE 3**

**Fig. 1**    *Retusotriletes*? *saturnus* sp. nov. BM 129970, proximal view, sample Arg92/10.

**Fig. 2**    *Telisporites* sp. A. LV92/13; **2a**, BM 130849, proximal view, × 500; **2b** BM 130850, distal spines and curvatural ridge; **2c** BM 130851, distinct sculpture on contact area, × 2500.

**Fig. 3**    *Insolisporites* sp. Ger92/2B; **3a**, BM 134643, proximal view showing distal sculpture and proximal apical cones; **3b**, BM 134644, detail of proximal apical sculpture, × 2000.

**Fig. 4**    *Raistrickia* sp. Ger15B; **4a**, BM 130714, proximal view, × 2000; **4b**, BM 130713, detail of baculate sculpture and labrate laesurae, × 2500.

**Fig. 5**    *Scylaspora vetusta* (Rodriguez) comb. nov. Ger2B/1; **5a**, BM 135149, obliquely compressed specimen with proximal crenulate muri near the equator; **5b** BM 135150, detail of proximal sculpture × 2000.

**Fig. 6**    *Emphanisporites* cf. *decoratus* Allen 1965. BM 132902, slightly oblique proximal view showing spaced distal cones, sample LV13/1.

**Fig. 7**    *Emphanisporites rotatus* McGregor 1961. BM 134062, proximal view, Arg92/5A.

**Fig. 8**    *Emphanisporites* cf. *splendens* Richardson & Ioannides 1979. BM 134633, proximal view?, showing annulus, apical thickening and radial muri, Ger92/2B.

**Fig. 9**    *Emphanisporites splendens* Richardson & Ioannides 1979. **9a**, BM 140339, proximal view showing well-developed paired lips, faint radial muri and three prominent inter radial thickenings, × 2000, LP10/DD; **9b**, BM136882, proximal view showing a kyrtome-like structure, Ger2B/1, × 1000. All figs × 1000, unless stated otherwise.
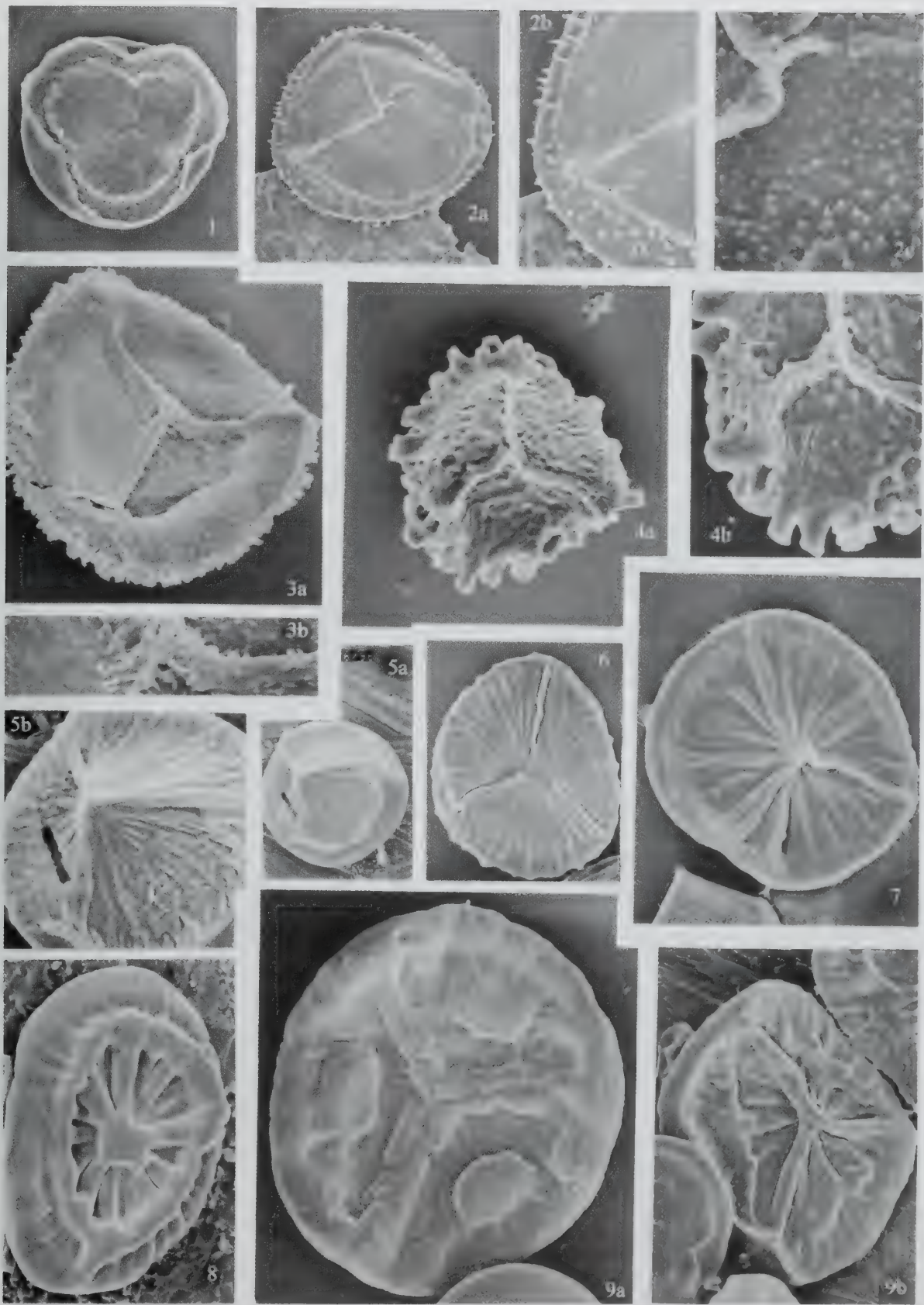
perfectae formed from sculptural elements and absence of sculpture outside the contact areas towards the amb and over the distal surface.

OCCURRENCE. Rare in the Cantabrian Mountains, Argovejo, La Vid, **hemiesferica (H)** to **micrornatus – newportensis (MN)** Biozones. Přídolí to Lochkovian. In England (Shropshire & Herefordshire) where this species occurs in the Lower Přídolí and spores of this type have been found also in sporangia (Fanning *et al.*, 1991: 3.2 b). Similar spores are found higher in the sequence in the Lower Lochkovian but the higher spores have a variably greater cover of apiculate to spinose sculpture; in extreme forms the spore is completely covered with cones/spines (Richardson, unpublished).

REMARKS. In the case of Form 2 the curvatural bands are defined by sculpture, sometimes barely discernible, sometimes forming broad bands of variable grana and coni paralleling the trilete mark and merging radially into curvatural sculpture. This species, *Apiculiretusispora arcidecus* sp. nov. occurs in the Lower Přídolí of England and has been found in sporangia (Fanning *et al.,* 1991). Stratigraphically higher spores are variable but include specimens with more pronounced sculpture. There is considerable variation; variants in the Lower Devonian have dense distal sculpture, whereas the proximal surface is completely covered with cones, or short spines, with only three small inter-radial areas remaining smooth (interradial papillae). A third species, *Breconisporites*? cf. *coronadus* shows that zonate spores may also have a distinct proximal pattern of sculpture similar to that of *A. arcidecus* sp. nov.

Genus *BRECONISPORITES* Richardson *et al.* 1982

*Breconisporites*? **spp.** (cf. *Retusotriletes coronadus* Rodriguez, 1983, *pars*) Pl. 2, figs 5–7; Pl. 4, figs 2–4

This form has equatorial wedge-shaped curvaturae extending equatorially (into a zona?). On the proximal surface there is a band of spines and cones in each of the inter-radial areas. These sculptured bands parallel the curvaturae and join with the sculpture which parallels the lips. The 'curvatural' sculpture is composed of fimbriae, spines and cones. Sculpture size *c.* 1–6 μm. The proximal central area, within the arcuate sculpture, may be depressed. There is a +/– circular thickening over the distal polar area.

REMARKS. Specimens of *Breconisporites* from South Wales (locus typicus) (Richardson *et al.,* 1982) have a bizonate cingulum and some species have a proximal area of coni; the Cantabrian spores

have some similarities but are not distinctly bizonate. Rare laevigate or proximally rugulate zonate spores that are more clearly bizonate occur near the top (sample LV 13) of the sampled part of the La Vid Section (Pl. 4, fig. 5). In specimens with prominent proximal spines (Pl. 4, fig. 3) the distribution of the spines, in arcuate, 'curvaturate' zones, linked to areas of spines bordering the lips, is similar to the pattern of sculpture seen in *Apiculiretusispora arcidecus* sp. nov. where the sculpture is much finer. The curvatural thickening is extended to form a zona and there are three arcuate bands of spines and cones on the proximal face. The latter spores, and the heavily sculptured spores of type 2, have been found only in the Devonian so far, and form part of a complex morphon, which is being further, investigated.

Infraturma **MURORNATI** Potonié & Kremp 1954
Genus *EMPHANISPORITES* McGregor 1961

TYPE SPECIES. *Emphanisporites rotatus* McGregor 1961 (Pl. 3, fig. 7).

*Emphanisporites splendens* Richardson & Ioannides 1979
Pl. 2, fig. 8, Pl. 3, fig. 9

1973 *Emphanisporites? pseudoerraticus* Richardson & Ioannides: 275–76, pl. 3, figs 12–15; pl. 4, figs 1–4, 7.
1978c *Emphanisporites? pseudoerraticus* Rodriguez: 417, pl. 2, fig. 17.
1979 *Emphanisporites splendens* Richardson & Ioannides: 111.
1983 ?*Emphanisporites pseudoerraticus* Rodriguez: 40, 41, pl. 3, fig. 20.

DIMENSIONS. 26–63μm (17 specimens); 50–78μm (24 specimens) (Richardson & Ioannides 1973).

REMARKS. The Cantabrian and North African specimens are highly variable, but the specimens in this study include much smaller forms than any found in North Africa. Also the 'annulus' is sometimes formed of three inter-radial tangential thickenings which together form a triangle resembling a proximal kyrtome. However, in some of the Cantabrian and the previously described North African specimens, there is no annulus but only irregular inter-radial thickenings. In other specimens (Pl. 3, fig. 8) with an annulus, radial ribs, and polar, or near polar, thickenings that may be proximal, there is no clear trilete mark. These are referred to herein as *Emphanisporites* cf. *splendens*.

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**PLATE 4**

**Fig. 1** *Aneurospora richardsonii* (Rodriguez) comb. nov. Tilt 45°, Arg97/13/1P; **1a,** BM 2118, oblique proximal compression; **1b,** BM 2119, showing distal coni, × 2000; **1c,** BM130290, specimen in oblique compression showing rigid equatorial crassitude, Arg/92/13.

**Fig. 2** *Breconisporites* sp. A. Sample La Vid 92/13/1; **2a,** BM 132895, proximal view; **2b,** BM 132896, distal proximal sculpture, × 2000.

**Fig. 3** *Breconisporites* sp. C. LV92/13/1; **3a,** BM 132899, proximal view; **3b,** BM 132900, spinose proximal sculpture forming zones parallel with the equator and paralleling the trilete sutures, × 2000.

**Fig. 4** *Breconisporites* sp. B. BM 130860, proximal view showing rugulate sculpture, × 500, LV92/13.

**Fig. 5** Zonate spore. Proximal view, specimen with laevigate contact face, BM 130859, LV92/13.

**Figs 6, 10** *Chelinospora* cf. *hemiesferica* (Cramer & Diez) comb. nov. **6,** BM 130308, Arg92/10; **6a,** BM 130307, oblique compression; **6b,** detail of radial folds around the hilum, × 2000; **10,** BM 132469, oblique view with spaced uncluttered distal muri, LP92/19.

**Fig. 7** *Chelinospora cantabrica* sp. nov. BM 135304, partial tetrad, upper specimen distal view showing large broad lacunae, lower specimen giving a partial proximal view of the equator surrounding hilate area and subequatorial sculpture, Ger92/2B/2.

**Fig. 8** *Chelinospora sanpetrensis* (Rodriguez) comb. nov. **8a,** BM 136891, distal view showing low muronate sculpture and narrow, occasionally branching lumena, Ger92/2B/3; **8b,** BM 135042, proximal/oblique view showing granulate – micro rugulate curvatural sculpture, thin broken hilum, and subequatorial radial lacunae, Ger92/2A; **8c,** BM 134063, spore tetrad showing sub-equatorial radial lacunae, sample Arg92/5A.

**Fig. 9** *Chelinospora hemiesferica* (Cramer & Diez) comb. nov. BM 132687, oblique view, LV92/10.

All figs × 1000, unless stated otherwise.

OCCURRENCE.    Lower and Middle San Pedro Formation, **RS** and **H** Biozones; Upper Ludfordian and Lower Přídolí, possibly some specimens are reworked.

Subturma **ZONOTRILETES** Waltz 1935 in Luber & Waltz 1938
Infraturma **CRASSITI** Bharadwaj & Venkatachala 1961
Genus *AMBITISPORITES* Hoffmeister 1959

## *Ambitisporites warringtonii* (Richardson & Lister, 1969) comb. nov.

BASIONYM.    *Retusotriletes warringtonii* Richardson & Lister 1969.

1969    *Retusotriletes warringtonii* Richardson & Lister 1969: pl. 37, figs 7, 8.

REMARKS.    The curvaturae are thickened and form a crassitude that is more or less coincident with the equator. These forms are closely similar to *A. avitus* except for the size and thickness of the crassitude.

## *Ambitisporites? eslae* (Cramer & Diez, 1975) comb. nov.
Pl. 5, fig. 1

BASIONYM.    *Retusotriletes eslae* Cramer & Diez 1975 (*pars*), 343, pl. 1, fig. 11 only.

  1973    *Ambitisporites* sp. B, Richardson & Ioannides: 277, pl. 6, fig. 8 only.
  1975    *Retusotriletes eslae* Cramer & Diez (*pars*): 343, pl. 1, fig. 11 only (see discussion under *Scylaspora elegans* sp. nov.).
?1976    *Retusotriletes maculatus* McGregor & Camfield: 26, pl. 1, fig. 6.
?1995    *Ambitisporites tripapillatus* Moreau-Benoit; Burgess & Richardson: 16, pl. 6, fig. 16.

HOLOTYPE.    Cramer & Diez 1975: pl. 1, fig. 11.

COMPARISON AND REMARKS.    *A. tripapillatus* Moreau-Benoit (1976: 37, pl. 7, figs 2–4) has a darkened area along the Y-rays at the spore apex with straight to concave sides. *Scylaspora elegans* has a large darkened apical area and proximal rugulate sculpture. *Retusotriletes maculatus* McGregor & Camfield (1976) and, in part, *Ambitisporites* sp. B (McGregor & Camfield, 1976: pl. 6, fig. 8 only), appear to have a narrow equatorial crassitude, but are otherwise similar to *A. eslae* (Cramer & Diez). They all show an equatorial crassitude except at the radial apices where the curvaturae invaginate. A similar feature is seen in some specimens of *Ambitisporites*, eg. *A. avitus*. Several Lower Devonian laevigate spores are proximally retusoid (McGregor & Camfield, 1976) and from the limited data available these spores appear to be pandemic, although many of

the records are from Spain, North Africa and South America. The age of similar spores to this species is varied. *A. eslae*, *A. tripapillatus* and *R.. maculatus* are all from the Lower Devonian but the Burgess & Richardson record is of Lower Přídolí age.

OCCURENCE.    Argovejo, **EC** (**a**) subzone and **MN** zone (Lower Lochkovian).

Genus *SCYLASPORA* Burgess & Richardson 1995

TYPE SPECIES.    *Scylaspora scripta* Burgess & Richardson 1995.

REMARKS.    Some of the spores placed in the genus *Rugosisporites* by Dufka (1995) resemble those of *Scylaspora*; however, the type species of *Rugosisporites* is *Retusotriletes chartulatus* McGregor (1978) which is retusoid with distinct invaginations at the radial apices. McGregor's species is similar, but not identical, to some Middle and Upper Devonian species also placed in the genus *Retusotriletes*, namely *R. rugulatus* and *R. phillipsii*. Consequently, since the type species of *Rugosisporites* is regarded here as belonging to *Retusotriletes*, as McGregor determined, then removal of the type species necessitates the invalidation of the genus *Rugosisporites* by placing it in synonymy with the genus *Retusotriletes*.

## *Scylaspora elegans* sp. nov.          Pl. 5, figs 2–4, Pl. 6, fig. 8

1975    *Retusotriletes eslae* Cramer & Diez (*pars*): 343, pl. 1, fig. 12 only.
1983    *Retusotriletes eslae* Cramer & Diez; Rodriguez, 1983: 47, pl. 5, figs 14, 19, 20.

HOLOTYPE.    FM 1490 (Pl. 5, fig. 2), diameter 43 µm; sample La Vid 13, slide D3/2, co-ord. 090 1036; E.F. no. J34/3; upper San Pedro Formation, La Vid section, Cantabrian Mountains, Province of León, northwest Spain.

DERIVATION OF NAME.    Latin a. elegans, refined, elegant, referring to the delicate proximal sculpture.

DIAGNOSIS.    A *Scylaspora* with a narrow +/– equatorial curvatural crassitude, three distinct proximal inter-radial papillae, Y-sutures bordered by darkened (?thickened) narrow areas tapering to the equator, proximal surface with contorted microrugulae, accompanied by short radial microrugulae near the curvaturae, microrugulae become less distinct polewards; distal exine laevigate.

DESCRIPTION.    Amb rounded to subtriangular. Proximal surface with straight to sinuous microrugulae adjacent to the curvaturae, <0.5 µm wide and high, and decreasing in height towards the proximal pole; straight microrugulae confined to the curvatural area. Under the SEM the microrugulae are close-packed and contorted

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**PLATE 5**

**Fig. 1**    *Ambitisporites? eslae* (Cramer & Diez) comb. nov. FM 1505, Arg92/12 (510) 3, 206 1169.

**Figs 2–4**    *Scylaspora elegans* sp. nov. **2**, FM 1490 (**holotype**), proximal view showing dark apical triangle, narrow crassitude, curvaturae perfectae and inter-radial papillae, LV92/13 (D3) 2, 0901036; **3a, 3b**, FM 1506, **3b**, × 1500 showing minute radial ridges outside the curvatural crassitude, Ger92/12 (371) 3, 100 1131; **4**, FM 1507, LV92/17 (D3) 3, co-ord. 207 0908, E.F.V21/3.

**Figs 5–8**    *Scylaspora vetusta* (Rodriguez) comb. nov. showing variations. **5**, FM 1508, oblique compression showing +/– radial muri around the curvatural crassitude, LV92/8 (D3) 2, 106 0991; **6**, FM 1509, proximal view, thin-walled specimen showing equatorial radial thickenings becoming indistinct towards the proximal pole, LP92/8 (D2) 1, 025 1014; **7a–c**, FM 1510, proximal view showing irregular and anastomosing proximal muri; **7c**, × 1500; LV92/8 (D3) 2, 058 1127; **8**, FM 1511, specimen showing paired lips, Arg92/5a (473) 3, 029 0910.

**Fig. 9**    *Scylaspora* cf. *scripta* Burgess & Richardson 1995. FM 1512, × 1500, LV97/8a (D16) 2, 096 1123.

**Fig. 10**    *Scylaspora* cf. *kozlica* (Dufka) comb. nov. FM 1513, LV92/8 (D3) 1, 163 0983; **10a**, proximal polar compression, showing proximal microrugulae and grana; **10b**, × 1500, showing detail of proximal sculpture.

All figs × 1000, unless stated otherwise.
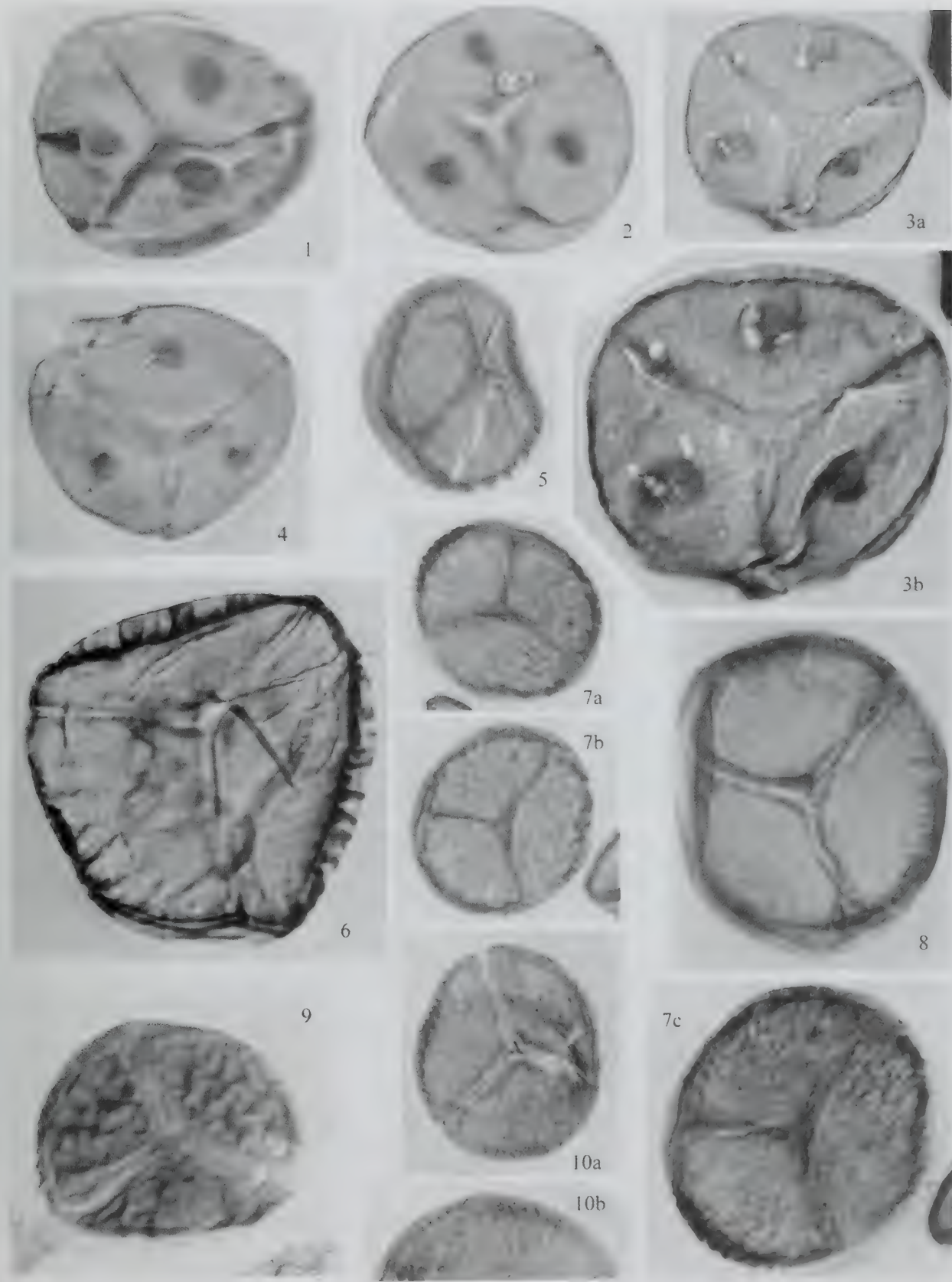
becoming sinuous, and less distinct, poleward. Trilete sutures +/– equal the spore radius or slightly less, accompanied by raised, often darkened areas, tapering towards the amb. A wider thinner proximal triangular area reaches c. 4/5ths of the spore radius and inter-radially often reaches the papillae; papillae distinct, rounded to ovoid in plan view, with a slightly raised profile, maximum diameter 4–9 μm. Trilete-folds, or smooth lips, occur in some specimens and are narrow over the apical area and expand towards the equator.

DIMENSIONS.    27–58 μm (59 specimens measured).

COMPARISONS.    *Scylaspora elegans* sp. nov. differs from proximally tripapillate *Ambitisporites* species by its proximal microrugulae and apical darkened area (lips) bordering the trilete mark. The photograph of the holotype of *Ambitisporites? eslae* Cramer & Diez (1975: pl. 1, fig. 11) lacks this feature and has a wide crassitude. *Retusotriletes maculatus* has proximal curvaturae invaginated at their radial apices.

REMARKS.    The current investigation revealed that *Retusotriletes eslae* Cramer & Diez includes two distinct forms. The original holotype has a broad equatorial crassitude, trilete folds and appears to lack the apical, gradually tapering and darkened areas that flank the trilete mark. Specimens with a broad crassitude are rare in the samples studied (eg. Pl. 5, fig. 1) and it is not known whether such forms have a proximal microverrucate sculpture. It has not been possible to study the holotype for this purpose and, although Cramer & Diez described microrugulae, their diagnosis states that the proximal surface is 'smooth to microrugulate'. Pending re-examination of the type material the forms with a broad crassitude are retained but referred to as *Ambitisporites? eslae* (Cramer & Diez). The more commonly occurring spores, with a narrow, more or less equatorial, curvatural crassitude, distinct trilete area and proximal microrugulae, are transferred to the new species *Scylaspora elegans*. The microrugulae can be seen under the light microscope in some specimens but under the SEM all spores of this species show microrugulae that decrease in size towards the proximal pole. Both species occur in all sections but data from the present study shows that *S. elegans* sp. nov. occurs at the base of the EC Biozone whereas *A? eslae* (Cramer & Diez) comb. nov. occurs first in the *Aneurospora* Subzone at the top of the EC Biozone. In the Cantabrian Mountains *Scylaspora elegans* sp. nov. occurs in strata equivalent to the Upper/uppermost Přídolí and extends into the Lower Lochkovian (Devonian) and may, therefore, help in establishing the Silurian/Devonian boundary.

OCCURRENCE.    Upper San Pedro Formation, Argovejo, Geras, La Peral and La Vid sections, **EC** Biozone to Lower **MN** Sub-Biozone, Upper Přídolí to Lower Lochkovian.

## *Scylaspora* cf. *scripta* Burgess & Richardson 1995
Pl. 5, fig. 9

DIMENSIONS.    23–29μm (3 specimens measured).

OCCURRENCE.    La Vid, samples 6, 7B, 8A.

## *Scylaspora vetusta* (Rodriguez) comb. nov.
Pl. 3, fig. 5; Pl. 5, figs 5–8; Pl. 6, fig. 1

BASIONYM.    *Archaeozonotriletes vetustus* Rodriguez, 1978b: 219, pl. 1, fig. 8.

| | | |
|---|---|---|
| 1973 | *Emphanisporites?* sp. D, Richardson & Ioannides (*pars*): 276, pl. 3, fig. 9 only. |
| 1978b | *Archaeozonotriletes vetustus* Rodriguez: 219, pl. 1, fig. 8. |
| 1978c | *Archaeozonotriletes chulus* Rodriguez: pl. 1, fig. 14. |
| 1978c | *Archaeozonotriletes vetustus* Rodriguez: 414, pl. 2, figs 7, 8. |
| 1983 | *Archaeozonotriletes vetustus* Rodriguez: 32, pl. 1, figs 2, 18, 20. |
| 1995 | *Rugosisporites* cf. *chartulatus* (McGregor); Dufka (*pars*): 71, pl. 2, figs 9–14. |

HOLOTYPE AND TYPE LOCALITY.    Rodriguez, R.M. 1978b: pl. 1, fig. 8; Corniero village, Province of León, Cantabrian Mountains, northwest Spain, lower San Pedro Formation, ?Ludfordian.

EMENDED DIAGNOSIS.    A *Scylaspora* with closely spaced, more or less radial, anastomosing, irregularly sinuous, muri/rugulae on the proximal surface; distally laevigate apart from a narrow subequatorial area with +/– radial muri.

DIMENSIONS.    28–72 μm (60 specimens measured).

REMARKS.    Spores of this species are highly variable. In some cases there are irregular muri/rugulae that reach the pole, in others cuneiform elements are prominent over the equatorial crassitude but sculpture is faint to indistinguishable over the rest of the proximal surface. Intermediates occur where distinct equatorial sculpture becomes increasingly faint leaving a laevigate apical zone. The equatorial crassitude is variable in width.

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**PLATE 6**

**Fig. 1**    *Scylaspora vetusta* (Rodriguez) comb. nov. **1a**, BM 140019, proximal view, LP92/10/DP; **1b**, BM 134179, proximal view showing subequatorial radial muri and scabrate apical area, sample Geras 92/7; **1c**, BM 134195, proximal view, showing irregular proximal sculpture, Arg92/4A/1.

**Fig. 2**    *Scylaspora* sp. BM 135151, strong broad equatorial crassitude and coarse sinuous proximal muri, Ger2B/2.

**Fig. 3**    *Coronaspora primordiale* (Rodriguez) Rodriguez 1983. BM 137485, proximal view showing inter-radial thickenings, grooved crassitude and lips, Ger2B/2.

**Fig. 4**    *Iberoespora cantabrica* Cramer & Diez 1975. **4a**, BM 116051, proximal view showing chevron-shaped elements forming the labra, Arg92/7; **4b**, BM 137480, proximal view showing inter-radial thickenings, Arg13/Dii.

**Fig. 5**    *Iberoespora glabella*? Cramer & Diez 1975. BM 129724, distal view showing concentric furrow inside equatorial crassitude and foveolate-muronate sculpture over central area, Arg92/11B.

**Fig. 6**    *Coronaspora cromatica* (Rodriguez) Jansonius & Hills 1979. **6a**, BM 134510, proximal view showing variably developed verrucate lips, kyrtome and inter-radial muri, Ger92/2B; **6b**, BM 134199, proximal view, showing kyrtome, inter-radial thickenings and verrucate labra, Arg5A/1; **6c**, BM 137269, distal view showing annulus and irregular muri in polar area, Ger92/2B/2; **6d**, BM 135144, oblique compression showing equatorial crassitude and distal annulus, Ger92/2B/1; **6e**, BM 134634, proximal view showing well-developed verrucate labra, Ger92/2B; **6f**, BM 134634, detail of proximal apical area in Fig. 6e, × 2000.

**Fig. 7**    *Coronaspora reticulata* sp. nov. **7a**, BM 138958, oblique proximal view showing kyrtome, LV92/7b/DD1; **7b**, BM 138395, proximal view showing kyrtome and thin apical area.

**Fig. 8**    *Scylaspora elegans* sp. nov. **8a**, BM 2548, proximal view, Arg 92/11B/2; **8b**, BM2551, detail of proximal microrugulae, tilt 45°, × 4000. All figs × 1000, unless stated otherwise.

*Scylaspora* cf. *kozlica* (Dufka) comb. nov.          Pl. 5, fig. 10

Cf. 1995 *Rugosisporites kozlicus* Dufka (*pars*): 72, pl. 2, figs 15–17.

DESCRIPTION.    Amb circular to subcircular. Equatorial crassitude 1–2 μm wide. Trilete mark labrate, *c.* 4/5 spore radius, lips less than 1μm wide, merge with curvaturae perfectae which form a narrow equatorial crassitude with a thicker inner portion and a narrow (< 0.5 μm), apparently membranous, extension. Proximal surface covered with narrow irregular rugulae *c.* 0.5 μm wide and possible micrograna. Sculpture less distinct near the proximal pole. Distal surface laevigate except for sub-equatorial rugulae with scattered micrograna.

DIMENSIONS.    31–44 μm (30 specimens measured).

COMPARISONS.    Similar to *S. scripta* in having radially aligned muri near the equator and distal sculpture, but has more radial geniculate and anastomosing robust muri. *S. kozlicus* (Dufka) is similar but is distally laevigate and lacks the paired lines of thickening on either side of the Y-mark. *S.* sp. A (this study) has geniculate muri on the proximal and distal surfaces and is rare.

REMARKS.    *Scylaspora* cf. *scripta* is similar to forms described from the Homerian and may be reworked. The spores have a membranous extension, seen at the equator on some specimens, and may be double-layered with the thin outer part of the exoexine forming the rugulae over the proximal surface. *S. vetusta* has coarser rugulae but is otherwise closely similar.

OCCURRENCE.    La Vid section, upper **RS** and lower **H** Biozones (Upper Ludfordian – Přídolí).

### Genus *CONCENTRICOSISPORITES* Rodriguez 1983

TYPE SPECIES.    *Concentricosisporites sagittarius* (Rodriguez) 1983.

REMARKS.    Jansonius & Hills (1990: card 4630) considered that the central dark area in the type species may represent an inner body.

*Concentricosisporites agradabilis* (Rodriguez) Rodriguez 1983                                                      Pl. 7, fig. 2

1978c   *Stenozonotriletes agradabilis* Rodriguez: 421, pl. 3, figs 7, 8, 11.
1983     *Concentricosisporites agradabilis* Rodriguez: 35, pl. 4, figs 7, 11, 13.

HOLOTYPE AND TYPE LOCALITY.    Rodriguez, 1978b: pl. 3, fig. 8; Torrestio, Province of León, Cantabrian Mountains, northwest Spain, lower San Pedro Formation.

DIAGNOSIS.    See Rodriguez, 1978c: 421.

DIMENSIONS.    26–39 μm (18 specimens measured); Rodriguez, 1978b, 24–35 μm.

COMPARISONS.    This species shows some resemblance to spores of the genus *Emphanisporites* but the proximal radial ribs are not always distinct and the equatorial crassitude is relatively wide (3–6 μm) in relation to the spore radius.

OCCURRENCE.    Lower San Pedro Formation; upper **RS** and lower **H** Biozones; sporadically occurs in **EC** and lower **MN** Biozones where they may represent reworking. In the higher specimens the distal annulus is lobed and the radial 'muri' more distinct. Upper Ludfordian and Lower Přídolí.

*Concentricosisporites sagittarius* (Rodriguez) Rodriguez, 1983                                                      Pl. 7, fig. 1

1978b   *Stenozonotriletes sagittarius* Rodriguez: 219, pl. 1, fig. 7.
1978c   *Stenozonotriletes sagittarius* Rodríguez: 421, pl. 2, figs 13, 14.
1983     *Concentricosisporites sagittarius* (Rodriguez); Rodriguez: 36, pl. 3, fig. 21.
1995     *Concentricosisporites sagittarius* Rodriguez; Burgess & Richardson: 17, pl. 6, figs 14, 15.

HOLOTYPE.    Rodriguez, 1978b: pl. 1, fig. 7.

DIAGNOSIS.    See Rodriguez, 1978b: 219.

DIMENSIONS.    29–44 μm (10 specimens measured); 25–40 μm (Rodriguez, 1978).

OCCURRENCE.    San Pedro Formation, Upper **RS** & **H** Biozones La Vid, upper **RS** & lower **H** Biozones La Peral, lower **MN** Biozone Geras (? reworked). Upper Ludfordian and Lower Přídolí.

### Genus *IBEROESPORA* Cramer & Diez 1975

TYPE SPECIES.    *Iberoespora cantabrica* Cramer & Diez 1975.

*Iberoespora cantabrica* Cramer & Diez 1975                                                      Pl. 6, fig. 4; Pl. 7, fig. 4

HOLOTYPE.    Cramer & Diez 1975: pl. 2, fig. 24.

DIAGNOSIS.    See Cramer & Diez 1975: 339, pl. 2, figs, 24, 26–28, 30, 31.

DIMENSIONS.    30 to 45 μm (Cramer & Diez, 1975); 27 to 42 μm (40 specimens measured).

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**PLATE 7**

**Fig. 1**   *Concentricosisporites sagittarius* (Rodriguez) Rodriguez 1983. FM 1514, Ger92/15a (475) 1, 044 1032.
**Fig. 2**   *Concentricosisporites agradabilis* (Rodriguez) Rodriguez 1983. FM 1515, LV92/13 (495) 2, 098 0982; **2a,** proximal focus; **2b,** distal focus, showing annulus.
**Fig. 3**   *Iberoespora glabella*? Cramer & Diez 1975. FM 1516, Argovejo 92/12 (510) 3, 139 0874.
**Fig. 4**   *Iberoespora cantabrica* Cramer & Diez 1975. FM 1517, Arg92/12 (510) 3, 212 0962; **4a, 4b,** showing verrucate lips, distal geniculate muri, and inter-radial thickenings; **4a,** × 1500; **4c,** median focus showing margin of the central body invaginated.
**Fig. 5**   *Leonispora argovejae* Cramer & Diez 1975. FM 1519, LV92/13 (D3) 1, 051 0913.
**Fig. 6**   *Iberoespora mariae* Rodríguez 1983. FM 1518, LP92/20 (D8) 2, Geras 92/11 (D8) 1, 030 0969 (see Fig.2, sample GER 11).
**Fig. 7**   *Aneurospora* sp. Tripapillate form. FM 1520, Ger92/14 (468) 7, 132 0975; **7a,** proximal focus; **7b,** proximal focus, showing curvaturae perfectae.
**Fig. 8**   *Streelispora newportensis* (Chaloner & Streel) Richardson & Lister 1969. FM 1521, LV13 (D3) 1, 082 0986; **8a, 8b,** × 1500.
**Fig. 9**   *Aneurospora richardsonii* (Rodriguez) comb. nov., FM 1522, Ger14 92/14 (468) 7, 135 0838; **9b,** shows sculpture in detail, × 1500.
**Fig. 10**   *Chelinospora sanpetrensis* (Rodriguez) comb. nov. FM 1523, Arg92/5a (473) 3, 123 1092; **10a,** distal focus showing foveolate exine; **10b,** with narrow arcuate fold around proximal hilum, × 1500.
    All figs × 1000, unless stated otherwise.
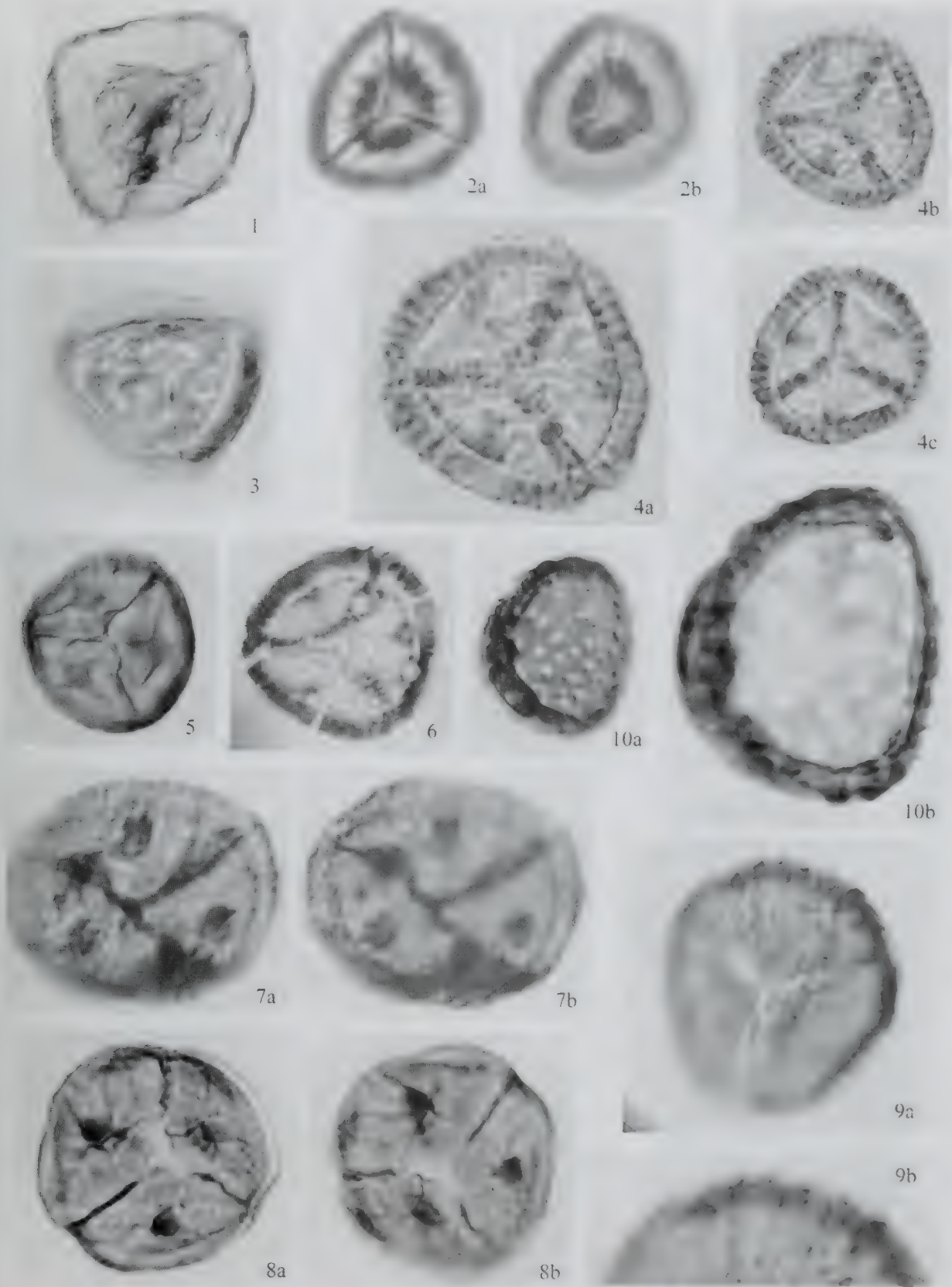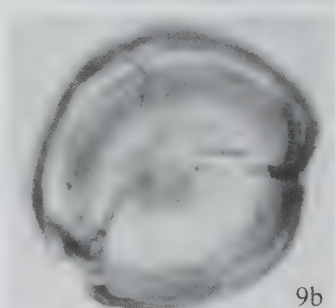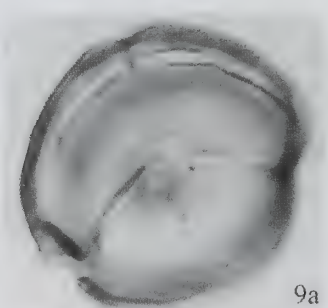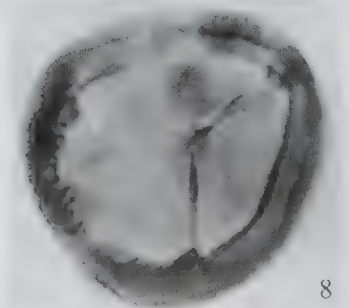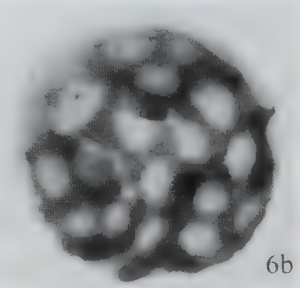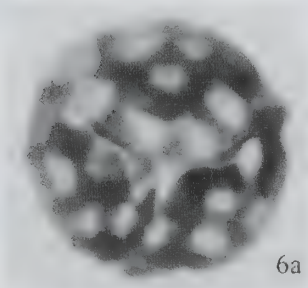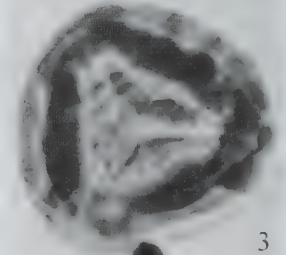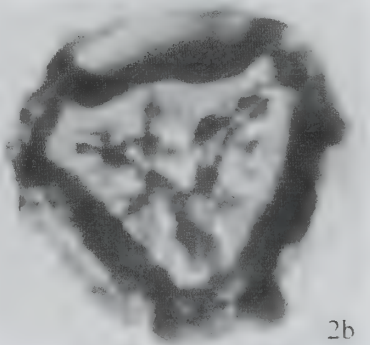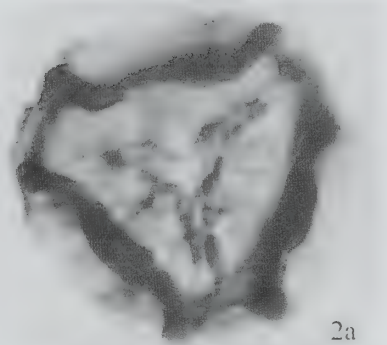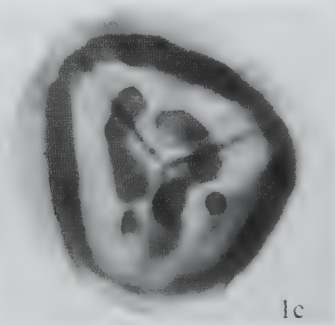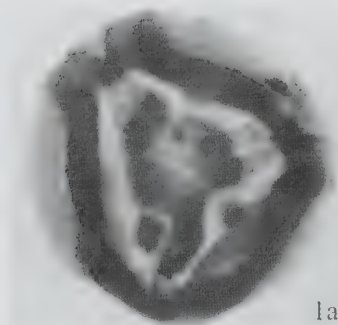
COMPARISON. Distally foveolate specimens with a laevigate crassitude are referred to as *Iberoespora glabella*? (Pl. 6, fig. 5; Pl. 7, fig. 3). The original illustrations (Cramer & Diez, 1975: pl. 2, figs 22, 29) do not show the distal surface clearly.

REMARKS. Cramer & Diez do not explain how they differentiate *I. guzmani* from *I. cantabrica*. Both species have the same structure, radial muri on the crassitude, crenulate lips, a distal sculpture of reticulate to convolute muri, and thickenings in the inter-radial areas. However, the size range given for *I. guzmani* is only 10–20 μm whereas that for *I. cantabrica* is 30–45 μm. The specimens in this study are all larger than 26 μm.

OCCURRENCE. Upper San Pedro Formation in Argovejo, Geras and La Vid sections in the Province of León and La Peral section in the Province of Asturias, upper **EC** – lower **MN** Biozones.

### Genus *LEONISPORA* Cramer & Diez 1975

TYPE SPECIES. *Leonispora argovejae* Cramer & Diez 1975.

*Leonispora argovejae* Cramer & Diez 1975          Pl. 7, fig. 5

HOLOTYPE. Cramer & Diez 1975, pl. 1, fig. 3.

DESCRIPTION. Cramer & Diez (1975: 342).

DIMENSIONS. 25–35 μm (ibid. 1975); 30–38 μm (14 specimens measured, present study).

COMPARISONS. The genus is closely similar in structure to *Streelispora* but is laevigate.

OCCURRENCE. Upper San Pedro Formation, Geras, La Vid sections; **MN** Miospore Biozone, **NA** Subzone.

### Genus *STREELISPORA* (Richardson & Lister) Richardson, Steel, Hassan & Steemans 1982

TYPE SPECIES. *Streelispora newportensis* (Chaloner & Streel); Richardson & Lister 1969.

*Streelispora newportensis* (Chaloner & Streel); Richardson & Lister 1969          Pl. 7, fig. 8

1968    *Granulatisporites newportensis* Chaloner & Streel: 92, pl. 19, figs 7, 8, 11.
1969    *Streelispora newportensis* (Chaloner & Streel); Richardson & Lister: 230–31, pl. 41, figs 3–6.

HOLOTYPE. Chaloner & Streel 1968: 92, pl. 19, figs 7, 8, 11.

DIMENSIONS. 28–39 μm (13 specimens measured), 17–48 μm (80 specimens measured) Richardson & Lister 1969.

OCCURRENCE. Upper San Pedro Formation, Argovejo, Geras, La Vid, **MN** Biozone, **NA** Sub-Biozone.

### Genus *ANEUROSPORA* Streel 1964

TYPE SPECIES. *Aneurospora goensis* Streel 1964

*Aneurospora richardsonii* (Rodriguez) comb. nov.
Pl. 4, fig. 1; Pl. 7, fig. 9

BASIONYM. *Streelispora richardsonii* Rodriguez, 1983: 50, pl. 8, figs 6, 7, pl. 9, fig. 3.

1978c   *Geminospora spinosa* Allen; Rodriguez: 416, pl. 5, figs 7, 8.
1983    *Streelispora richardsonii* Rodriguez: 50, pl. 8, figs 6, 7, pl. 9, fig. 3.

HOLOTYPE AND LOCUS TYPICUS. See Rodriguez, 1983: 50, pl. 8, fig. 3.

EMENDED DIAGNOSIS. An *Aneurospora* with no proximal papillae, distal sculpture consists of spaced slender spines (fimbriae), elements dominantly parallel-sided with blunt, rounded apices.

COMPARISON. The slender fimbriae distinguish this species. *Anapiculatisporites raistrickiaeformis* Schultz (1968) has coarser, more irregular elements (see also Steemans 1989).

DIMENSIONS. 38 to 50 μm (Rodriguez, 1983); 32 to 47 μm (28 specimens measured).

OCCURRENCE. Lower part of lower **MN** Biozone, NA Subzone, Argovejo, Geras and La Vid sections.

REMARKS. The species *Aneurospora richardsonii* lacks the proximal papillae and associated tangential folds and is herein transferred to the genus *Aneurospora*. Tangential folds around the proximal papillae distinguish *Streelispora* and *Leonispora* from tripapillate species of *Aneurospora* (eg. Pl. 7, fig.7).

### Genus *CORONASPORA* Rodriguez 1979 emend.

1978b   *Coronaspora mariae* Rodriguez: 218, pl. 1, figs 1–3.
1979    *Coronaspora mariae* Rodriguez: 232.

TYPE SPECIES. *Coronaspora mariae* Rodriguez, 1978.

HOLOTYPE. *Coronaspora mariae* Rodriguez, 1978b: pl. 1, figs 1, 2.

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**PLATE 8**

Figs 1–4   *Coronaspora cromatica* (Rodriguez) emend. **1,** FM 1524; **1a,** showing proximal kyrtome and broad verrucate lips. **1b,** intermediate focus. **1c,** distal view showing annulus and sculpture of sinuous muri and rounded verrucae; Ger92/5 (542) 2, 098 1006; **2,** FM 1525; **2a–c,** proximal to distal levels of focus; **2a** with narrow lips and distinct kyrtome; **2b** relatively narrow crassitude; **2c,** distal sculpture of small interconnected narrow verrucae Arg92/5a, (473) 3, 023 0983; **3,** FM 1526, proximal view, Arg92/5a (473) 3, 139 1133; **4,** FM 1527, proximal view, specimen with inter-radial thickenings on the kyrtome, Arg92/5a (473) 3, 099 0938.

Figs 5, 6   *Coronaspora reticulata* sp. nov. **5,** FM 1528, proximal focus showing kyrtome with wide inter-radial thickenings, LV92/7b (D3) 3, 156 0917; **6a, b,** FM 1491 **(holotype)**, showing distal reticulum (the radial extremities are visible in Fig. 6a), LV92/7b (D3) 3, 043 0965.

Fig. 7   *Coronaspora subornata* (Cramer & Diez) comb. nov. FM 1529, specimen showing narrow Y-folds, equatorial crassitude, distal annulus and irregular distal thickening; Ger92/9 (456) 1, 035 0472.

Fig. 8   *Chelinospora canistrata* sp. nov. FM 1492 **(holotype)**, Ger92/5 (542) 2, 083 1024.

Fig. 9   *Coronaspora infraornata* (Rodriguez) comb. nov. FM 1530, showing curvatural crassitude, distal annulus and distal polar thickening at two focal levels, Ger92/9 (456) 1, 066 0942.
All figs × 1000.

EMENDED DIAGNOSIS. Equatorial crassitate miospores with rounded or convexly triangular amb, a proximal kyrtome of thickened arcuate ridges extending to the radial apices where it is flat-topped and joins with the trilete lips; distal surface with, or without, a distal annulus; distal exine laevigate, verrucate, irregularly murornate, or reticulate.

COMPARISON. The rounded amb and distinct kyrtome distinguish this genus. There is no kyrtome on the type species of *Amicosporites* (*A. splendidus*) but two other species, *A. infraornatus* Rodríguez 1978b and *A. subornator* Cramer and Díez 1975 have this structure and are herein transferred to *Coronaspora*. The kyrtome in *Ahrensisporites* Potonié & Kremp, 1954 and *Concavisporites* Pflug in Thomson and Pflug, 1953 are distinct because the radial parts are prominent and inter-radially the amb is straight to concave. The kyrtome tapers evenly towards the equator in *Kyrtomisporis* Mädler 1964 (see also Achilles, 1981) whereas in *Coronaspora* the kyrtome is a radially broad and flattened (truncated) thickening where the inter-radial branches of the kyrtome meet, and may invaginate to become confluent with the lips. In cross-section the Silurian kyrtomes have a semicircular-shape.

REMARKS. Rodriguez validated the genus in 1979 when she designated *Coronaspora mariae* as type species.

### *Coronaspora cromatica* (Rodriguez) emend
#### Pl. 6, fig. 6; Pl. 8, figs 1–4

1978b   *Coronaspora cromatica* Rodríguez: 218, pl. 1, fig. 4.
1979    *Coronaspora cromatica* (Rodriguez) Jansonius & Hills: card number 3543.
1983    *Coronaspora cromatica* Rodríguez: pl. 3, fig. 4.

HOLOTYPE. Rodriguez, 1978b: 218, pl. 1, fig. 4.

EMENDED DIAGNOSIS. A *Coronaspora* with distinct labra, a proximal kyrtome with inter-radial thickenings, distal annulus, and variable muri and verrucae in the distal polar region.

DESCRIPTION. Amb subcircular to subtriangular with convex sides. Spores preserved in polar compression suggesting an original of more or less lenticular shape. Exine proximally with a distinct complete kyrtome with inter-radial thickenings, radial 'bars', connecting these to a narrow (*c.* 3 μm), +/– smooth to irregularly thickened, equatorial crassitude. Kyrtome distinct, formed by raised ridges (+/– semi-circular in profile) paralleling the lips in the inter-radial areas, flattened at radial extremities where it may show distinct invaginations; lips variably developed, may be broad and verrucate often taper sharply to the apices, or may be laevigate and sinuous; in forms with verrucate lips sutures distinct. Distally an annulus has smooth to irregular margins *c.* 9 μm wide, outer border

of annulus reaches to 2/3 of the spore radius. Distally polar area sculptured by broad muri 3–7μm wide, 9–18 μm long, muri highly variable in shape and orientation, forming linear or sinuous bars which may be smooth-sided, or show a series of constrictions giving a beaded appearance, due to the mixture of verrucae and short muri, or coalescent verrucae.

DIMENSIONS. 28–47 μm (58 specimens measured); Rodriguez, 1978b, 20–30 μm; width of the cingulum *c.* 2 μm.

COMPARISONS. *Coronaspora mariae* also has a distal annulus and is closely similar but has large rounded verrucae over the distal pole.

REMARKS. Rare specimens with sinuous laevigate lips, like the type material (Rodriguez, 1978b), occur in the Upper part of the San Pedro Formation. So far the forms with smooth lips have only been found in the upper **H** to **EC** Zones. Specimens with verrucate lips occur in the upper **RS** Zone and may prove to be a useful marker for the lower boundary of the Přídolí.

OCCURRENCE. Forms with verrucate lips (Pl. 6, fig. 6, Pl. 8, figs 1–4) occur in the Lower San Pedro Formation; lower upper **RS** Biozone Geras, Argovejo, lower **H** La Vid and La Peral sections; spores with laevigate lips, *C.* cf. *cromatica*, Upper San Pedro Formation, upper **H** & **EC** Biozone La Peral, **EC** & lower **MN** Biozones La Vid.

### *Coronaspora reticulata* sp. nov. Pl. 6, fig. 7; Pl. 8, figs 5, 6

1975    *Knoxisporites? riondae* Cramer & Diez (*pars*): 341, pl. 1, fig. 17 only.
1978c   *Knoxisporites? riondae* Cramer & Diez; Rodriguez : 42, 43, pl. 2, figs 18, 19.
1983    *Knoxisporites? riondae* Cramer & Diez; Rodriguez (*pars*): 42, 43, pl. 4, figs 2, 3.

HOLOTYPE. FM 1491 (Pl. 8, fig. 6), diameter 36 μm; sample La Vid 7B, slide D3/3, co-ord. 043 0965; E.F. no. E27/1; lower San Pedro Formation, La Vid section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Coronaspora* with broad distal muri forming a reticulum; kyrtome thickened especially in the inter-radial areas; kyrtome surrounds a clover-leaf shaped area of thin exine; laesurae labrate, labra narrow, smooth and sinuous.

DESCRIPTION. Amb circular to subcircular. Spores usually preserved in polar compression, suggesting an original, more-or-less lenticular cross-section. Equatorial crassitude smooth +/– 2 μm. Kyrtome smooth, invaginated and increasing in width towards the spore apex in the inter-radial areas, 2–4 μm, joined at the radial apices where they may be slightly invaginated at the junction with

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**PLATE 9**

**Fig. 1**  *Chelinospora cantabrica* sp. nov. FM 1493, **(holotype)**; **1a**, distal focus showing a reticulum of broad muri, several with characteristic narrow restrictions; **1b**, shows equatorial margin and muri in plan, Arg92/5a (473) 3, 144 1082.

**Fig. 2**  *Chelinospora lavidensis* sp. nov. FM 1494 **(holotype)**, showing narrow muri forming an irregular reticulum with subequatorial muri normal to the equator, Arg92/12 (510) 3, 093 1019.

**Figs 3, 5**  *Chelinospora hemiesferica* (Cramer & Diez) comb. nov. **3**, FM 1531; **3a**, proximal view showing thick crassitude and narrow concentric fold at the equatorial edge of the hilum; **3b**, distal surface showing close-packed narrow geniculate muri, Ger92/9 (450) 1, 147 1050; **5**, FM 1532 tetrad, showing parallel subequatorial muri normal to the equator and geniculate muri over the distal patina, Arg92/14 (468) 11, 080 1069.

**Fig. 4**  *Chelinospora* cf. *hemiesferica* (Cramer & Diez) comb. nov. **4**, FM 1533; **4a**, distal view, muri geniculate, but broader and more spaced than in the species; **4b**, proximal focus showing margins of the hilum, Arg92/11a (441) 4, 074 0915.

**Fig. 6**  *Chelinospora media* sp. nov. FM 1495, holotype, Arg92/12 (510) 3, 093 1019.

**Fig. 7**  *Cymbosporites* cf. *dittonensis* Richardson & Lister 1969. FM 1534, Arg92/13 (455) 1, 049 1014.
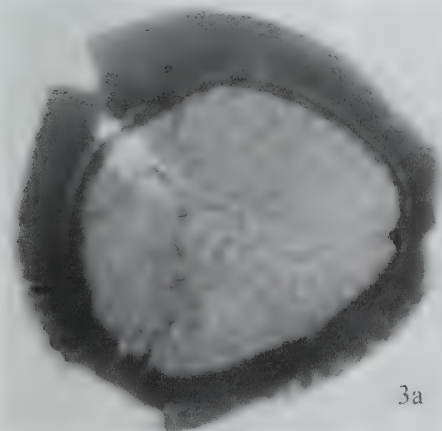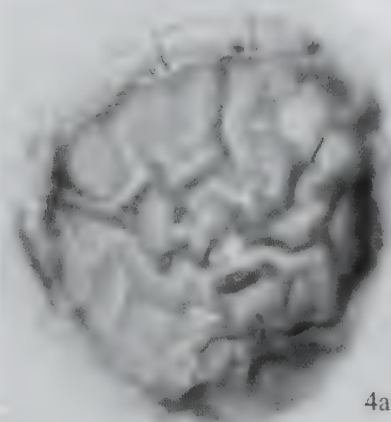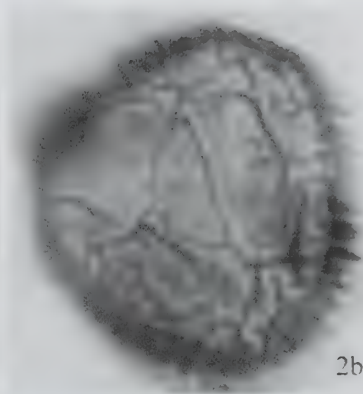
All figs × 1000.
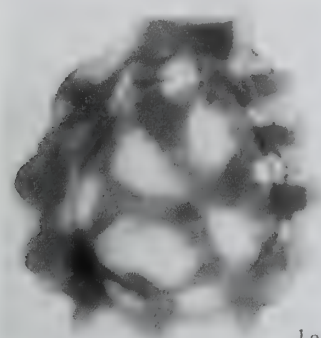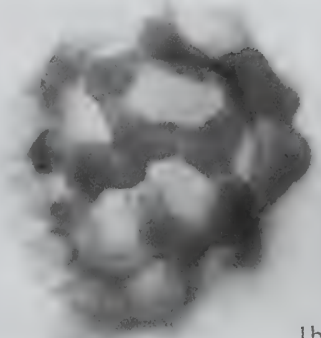
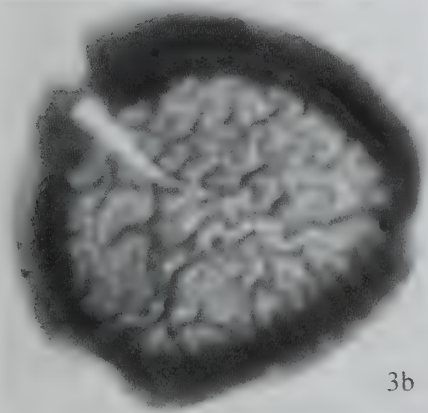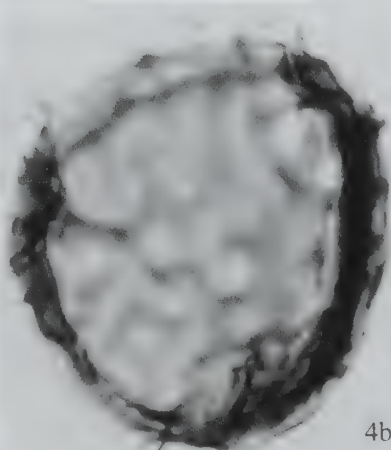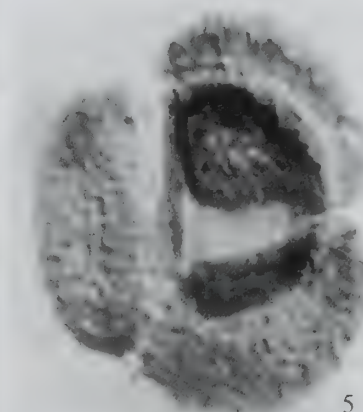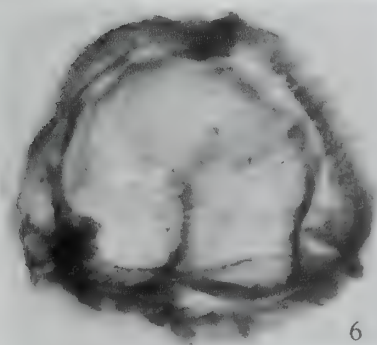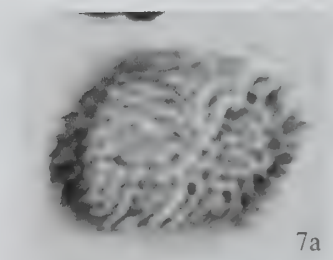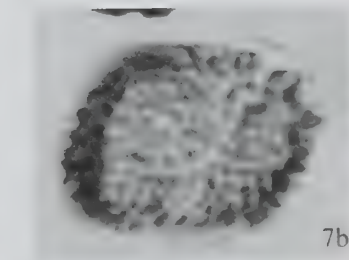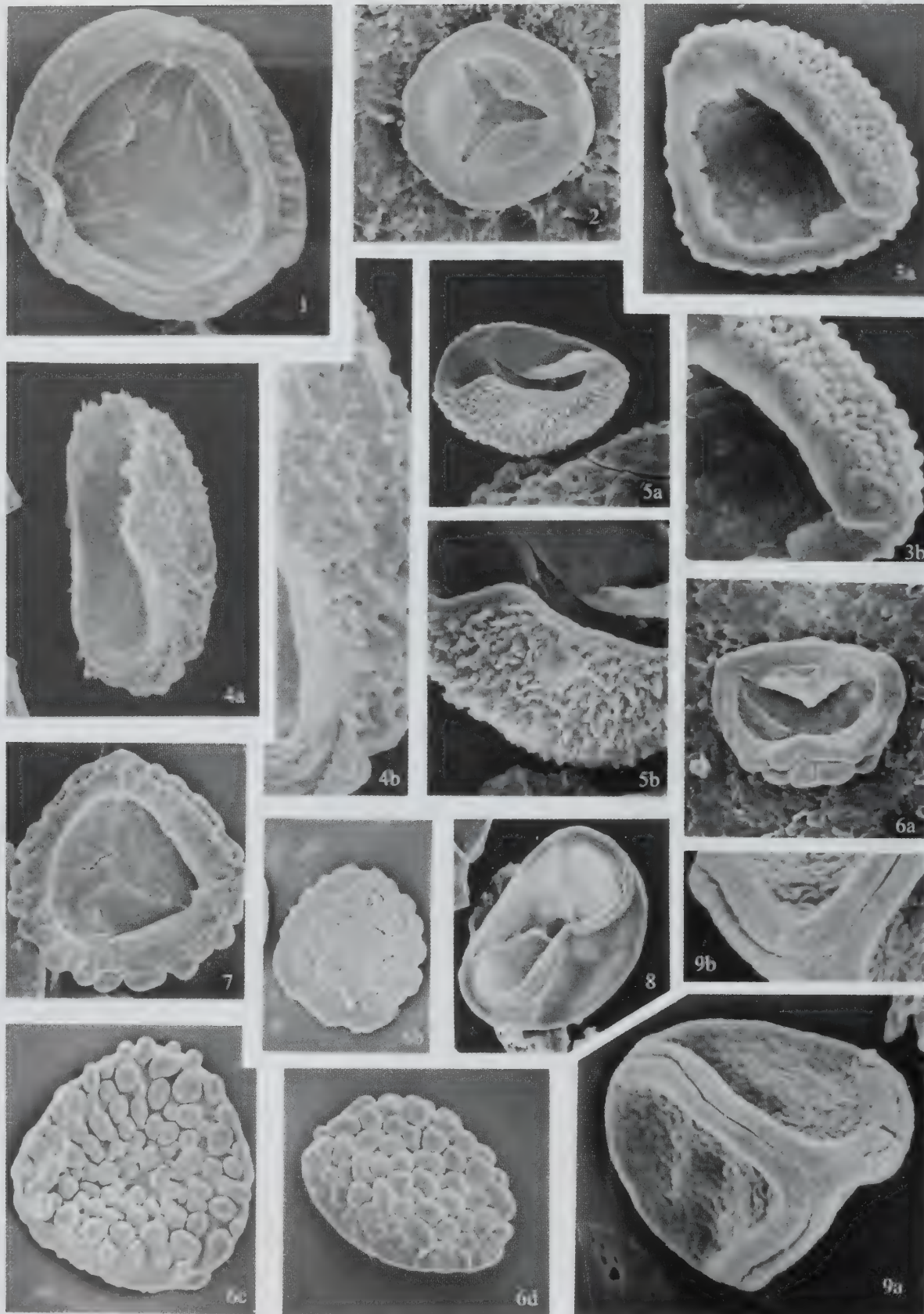the laesurae, lips smooth, narrow, decreasing in width over the thinner polar area, <1 μm wide. Distal surface with a reticulum of broad muri c.1–4 μm wide and *c.* 1 μm high, surrounding +/– polygonal lumine 3–6 μm maximum width.

DIMENSIONS.   26–44 μm (52 specimens measured).

COMPARISONS.   The presence of an equatorial crassitude, proximal kyrtome and distal reticulum, distinguish this species from *Knoxisporites? riondae* Cramer & Diez 1975, the latter has a 'marked concentric ring' around the distal pole and distal warts (see Cramer & Diez 1975: 341, reconstruction fig. 2.3, and distal focus of holotype pl. 1, fig. 16).

REMARKS.   The proximal surface is seen best under the SEM (Pl. 6, fig. 7b) but the kyrtomal thickenings and thin trilobed proximal apical area are also seen under the light microscope.

OCCURRENCE.   La Peral **RS** and lowermost **H** Biozone, La Vid **RS** Biozone, and doubtful, poorly preserved specimens in upper **EC** and lower **MN** Biozones; Upper Ludfordian and Přídolí; possibly re-worked in Upper Přídolí and Lower Lochkovian, Argovejo.

## *Coronaspora subornata* (Cramer & Diez) comb. nov.
Pl. 8, fig. 7

BASIONYM.   *Amicosporites subornator* Cramer & Díez 1975: 338, pl. 1, fig. 7.

1973    Spore type D; Richardson & Ioannides: 281, pl. 9, fig. 2.
1975    *Amicosporites subornator* Cramer & Díez: 338, pl. 1, fig. 7.
1978c   *Amicosporites subornator* Cramer & Diez; Rodriguez: 412–13, pl. 2, fig. 2.
1983    *Amicosporites subornator* Crame & Diez; Rodriguez: 30, pl. 3, fig. 13.

HOLOTYPE.   Cramer & Diez 1975; pl. 1, fig. 7; San Pedro Formation, Argovejo section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS.   A *Coronaspora* with a distal annulus and smooth exine.

Description.   Amb subcircular to subtriangular with convex sides. Spores preserved in polar compression, suggesting an original of more or less lenticular shape. Exine with a distinct proximal kyrtome, equatorial crassitude +/– smooth to irregularly thickened, and a narrow distal annulus (*c.* 3 μm wide); annulus smooth, and reaches to *c.* 4/5 of the spore radius. Distal? pole surrounded by a dark ring (?annulus). Trilete sutures reach the crassitude, which is invaginated at the radial apices; lips smooth, distinct, and parallel-sided.

DIMENSIONS.   30–40 μm (Cramer & Diez, 1975); 31–44 μm (14 specimens measured, present study).

COMPARISONS.   Differs from other members of the genus, with the exception of *C. infraornata*, in having a laevigate exine, *C. infraornata* has a dark distal polar area.

REMARKS.   Cramer & Diez (1975: 338) refer to the kyrtome as 'three segments of a circular inspissation' and a dark polar ring as a proximal inspissation. The spores differ from typical members of the genus *Amicosporites* because they have a distinct proximal kyrtome (Cramer & Diez, 1975; fig. 2, 2) similar, if not identical, to those of *C. mariae* and *C. cromatica*. We therefore transfer this species to *Coronaspora*.

OCCURRENCE.   La Peral **EC** Biozone, La Vid, uppermost **H**, or lowermost **EC** Biozone, Argovejo, **H** Biozone; Middle and Upper Přídolí.

## *Coronaspora infraornata* (Rodriguez) comb. nov.
Pl. 8, fig. 9

BASIONYM.   *Amocosporites infraornatus* Rodríguez 1978b: 217, pl. 1, figs 5, 6.

1978b   *Amocosporites infraornatus* Rodríguez: 217, pl. 1, figs 5, 6.
1978c   *Amocosporites infraornatus* Rodriguez: 412, pl. 2, fig. 3.
1983    *Amocosporites infraornatus* Rodriguez: 29, pl. 2, figs 14, 16.

HOLOTYPE.   Rodriguez, 1978b: 217–18, pl. 1, figs 5, 6; San Pedro Formation, Corniero section, Province of León, Cantabrian Mountains, northwest Spain.

EMENDED DIAGNOSIS.   A *Coronaspora* with a distal annulus, smooth exine, and a dark circular area over the distal pole.

DESCRIPTION.   Amb subcircular to subtriangular with convex sides. Spores preserved in polar compression, suggesting an original of more or less lenticular shape. Exine with a distinct proximal kyrtome, equatorial crassitude +/– smooth to irregularly thickened, and a narrow distal annulus; annulus smooth and 2–3 μm wide, reaches to *c.* 4/5 of the spore radius. Distal pole surrounded by a circular dark area. Trilete sutures reach the crassitude, which is invaginated at the radial apices; lips smooth, distinct, and parallel-sided.

DIMENSIONS.   15–35 μm Rodriguez (1978b); 25–47 μm (25 specimens measured, present study).

COMPARISONS.   Differs from *Coronaspora subornata* in having the circular dark area at the distal pole. In the present study, forms with a dark ring can be distinguished from those with a circular dark area

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**PLATE 10**
**Fig. 1**  *Chelinospora hemiesferica*? (Cramer & Diez) comb. nov. BM 137697, proximal view, × 2000, Ger92/9/D1.
**Fig. 2**  ?*Cymbosporites* sp. A. BM 134646, proximal view, Ger92/2A.
**Fig. 3**  *Cymbosporites* sp. B. Arg92/10; **3a**, BM 130309, proximal/oblique view, × 2000; **3b**, BM 130310, detail of sculpture showing some grana fused into groups, × 2500.
**Figs 4, 5**  *Cymbosporites* sp. **4a**, BM 133533, Ger92/14, equatorial view; **4b**, same specimen showing detail of multi-layered wall structure and acinoform sculpture of muri and microconi, × 2000; **5**, sample Geras 92/8; **5a**, BM 130610, equatorial view; **5b**, BM 130611, detail of irregular distal coni, × 2000.
**Fig. 6**  *Chelinospora (Lophozonotriletes?) poecilomorpha* (Richardson & Ioannides) comb. nov. **6a**, BM 135046, oblique compression showing hilum and large distal verrucae. Ger92/2A; **6b**, BM 141007, proximal view. LP10/DD2; **6c**, BM 132242, distal view, Arg92/13, BM 116097; **6d**, distal view showing discrete, rounded to flat-topped verrucae variable in size, LP92/16.
**Fig. 7**  *Chelinospora (Lophozonotriletes?) poecilomorpha* (Richardson & Ioannides) comb. nov. BM 141007, proximal view, LP92/10/DD2.
**Fig. 8**  *Archaicusporites torrestionensis*? Rodriguez 1983. BM 130522, proximal/oblique view, Ger92/9.
**Fig. 9**  Cf. *Pachytetras* sp. Possible permanent cryptospore tetrad. Ger92/2B/2; **9a**, BM 137274, tetrad showing rugulate distal sculpture; **9b**, BM137275, triple contact.
All figs × 1000, unless stated otherwise.

but in the original description Rodriguez separated *Amicosporites infraornator* from *A. subornata* on the distal position of the dark area. Cramer & Diez (1975) on the other hand thought that the dark ring in *A. subornator* was proximal. If further specimens show that in *A. subornator* the dark ring is distal then the two species may have to be combined.

REMARKS. The spores differ from typical members of the genus *Amicosporites* in having a proximal kyrtome (see under *C. cromatica*). Rodríguez (1978b) included in her species both spores with a distal annulus, not well defined at the inner margin, and others where the annulus was dissected into a series of verrucate-like structures (Rodríguez, 1978b: pl. 1, fig. 12).

OCCURRENCE. Geras, upper **RS, H** and lower **EC** Biozones, La Vid, upper **RS** to top **H** Biozones, Argovejo, **RS, H, EC** and **MN** Biozones, La Peral upper **H** and lower **EC** Biozones; Přídolí and lowermost Devonian.

Infraturma **PATINATI** Butterworth & Williams 1958 emend.
Smith & Butterworth 1967
Genus *CHELINOSPORA* Allen 1965

TYPE SPECIES. *Chelinospora concinna* Allen 1965.

## *Chelinospora canistrata* sp. nov.                     Pl. 8, fig. 8.

DERIVATION OF NAME. Latin *canistrum* n. wicker basket, canistrata resembling a basket.

HOLOTYPE. FM 1492, sample Geras 92/5, slide 2 (542), co-ord. 0831024, E.F. no. J33/1; Lower San Pedro Formation, Geras section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with low large verrucae-muri and closely packed convolute microrugulae.

DESCRIPTION. Proximally hilate, distally patinate miospores; hilum thin, sometimes diaphanous, frequently torn, or may be collapsed or lost, with a narrow concentric fold just inside the crassitude; narrow equatorial curvatural crassitude with short proximal radial muri extending to the hilum margin seen on a few specimens; distal sculpture of low verrucae and muri, often indistinct, and closely packed sinuous microrugulae < 1 μm wide. Y-mark with narrow 'folds' extend *c*. 2/3 spore radius and merge into crassitude at the hilum margin.

DIMENSIONS. 25–43 μm (based on 18 specimens).

COMPARISONS. The sculpture of low verrucae-muri and microrugulae distinguish *Chelinospora canistrata* sp. nov. from

other *Chelinospora* species.

OCCURRENCE. Found in all sections apart from La Vid, uppermost **RS, H**, and lower **EC** Biozones.

## *Chelinospora cantabrica* sp. nov.     Pl. 4, fig. 7; Pl. 9, fig. 1

DERIVATION OF NAME. Named after the Cantabrian region, NW Spain.

HOLOTYPE. FM 1493 (Pl. 9, fig. 1), diameter 39 μm, sample Argovejo 92/5a, slide 3 (473), co-ord. 1441082, E.F. no. P39/1; Lower San Pedro Formation, Argovejo section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with a reticulum composed of broad muri with occasional constrictions and narrow sutures, lumina wide, polygonal to irregular.

DESCRIPTION. Proximally hilate miospores, equatorially 2–4 μm thick, distal exine thick (not measured); amb subcircular to subtriangular. Proximal exine thin, frequently broken, or absent, trilete mark not seen. Equatorially and distally sculptured with a broad reticulum, muri 1–10 μm wide, 1–3 μm high, lumina wide and polygonal 2.5–10 μm wide; muri show constrictions broken by narrow sutures at the junction with adjacent polygonal fields.

DIMENSIONS. 5–51 μm (based on 20 specimens).

COMPARISONS. The broad muri with distinct constrictions and sutures, and wide +/– polygonal lumina, distinguish this species from other species of *Chelinospora*. *Coronaspora reticulata* sp. nov. has similar reticulate sculpture but has an equatorial crassitude and a proximal kyrtome.

OCCURRENCE. Argovejo, Geras, and La Vid sections, Lower San Pedro Formation, **RS** and lowermost **H** Biozones, occasional finds in higher zones in the La Vid section.

## *Chelinospora cassicula* Richardson & Lister 1969

1969    *Chelinospora cassicula* Richardson & Lister: 242–43, pl . 42, figs 10–12.
1978a  *Chelinospora mariae* Rodriguez (pars); Rodriguez: 10, pl. 1, fig. 3 only.

REMARKS. Rodriguez, 1978a (pl. 1, figs 3–5) placed several spore morphologies in this taxon but from the illustration the holotype belongs in *C. cassicula*.

In the Spanish material examined for this paper several *Chelinospora* species with an equatorial band of radial muri form an evolving 'lineage' (morphon) beginning with *C. hemiesferica*,

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**PLATE 11**

Fig. 1    *Conochitina pachycephala* Eisenack 1964. FC 90l, lateral view, × 170, LP3/SB4/45.
Fig. 2    *Conochitina alargada* Cramer 1967. FC 91, lateral view, × 220, Arg4/SB7/3.
Figs 3, 5, 6    *Cyathochitina elenitae* Cramer 1964. **3,** FC 92, lateral view, × 200, LP3/SB4/48; **5,** FC 93, lateral view × 200, Arg4/SB7/3; **6,** FC 94, Arg3/SB7/1; **6a,** lateral view × 150; **6b,** detail of carina, × 750.
Fig. 4    *Spinachitina* sp. FC 95, LP2/SB4/43; **4a,** lateral view, × 300; **4b,** basal margin detail, × 1750.
Fig. 7    *Calpichitina velata* (Wrona 1980). FC 96, Ger15b/SBGeras-1; **7a,** apertural view, × 500; **7b,** detail of operculum × 1000.
Fig. 8    *Vinnalochitina horrentis* (Jaglin 1986). FC 97, Ger13/SBGeras-2; **8a,** apertural view, × 500; **8b,** detail of operculum × 1000.
Fig. 9    *Cingulochitina wronai* Paris & Kríz 1984. FC 98, lateral view, × 500, Arg7/541/2, (R/34).
Fig. 10    *Urnochitina urna* Eisenack 1934. FC 99, lateral view, × 300, LP20/SB5/55.
Fig. 11    *Cingulochitina ervensis* (Paris 1979). FC 100, Ger11/458/7, (N31/2); **11a,** lateral view, × 250; **11b,** detail of carina, × 1000.
Fig. 12    *Cyathochitina* sp. B, Paris 1981.FC 101, Arg3/SB7/1; **12a,** lateral view, × 300; **12b,** detail of carina, × 800.
Fig. 13    ?*Margachitina catenaria* Obut 1973. FC 102, apertural view, × 400, Ger16/471/3.
Fig. 14    *Eisenackitina bohemica* (Eisenack 1934). FC 103, lateral view, Ger14/468/14, (Q26/4).

followed by *C.* cf. *hemiesferica* in the **H** Biozone, accompanied by *C. lavidensis* in the upper part of the **H** zone. *Chelinospora media* and *C. cassicula* are confined to the higher parts of the section studied Lower Lochkovian (upper **EC** & lower **MN** Biozones).

OCCURRENCE.    Argovejo, Geras, and La Vid sections Upper San Pedro Formation, lower **MN** (**NA**) Sub-Biozone.

## *Chelinospora hemiesferica* (Cramer & Diez) comb. nov.
Pl. 4, fig. 9; Pl. 9, figs 3, 5

BASIONYM.    *Iberoespora hemiesferica* Cramer & Diez, 1975: 341, pl. 2, figs 34–36.

1978c    *Cymbosporites dittonensis* Richardson & Lister; Rodriguez: pl. 3, fig. 18.

HOLOTYPE AND LOCUS TYPICUS.    Cramer & Diez 1975: 334, 336; pl. 2, figs 34, 35: 'base of a thick green shale 10 m below the exposed top of the San Pedro Formation at the westernmost outcrop in the village of Argovejo in the province of León, Spain'.

EMENDED DIAGNOSIS.    A *Chelinospora* with closely spaced narrow muri, geniculate in plan, over the distal hemisphere and an equatorial to subequatorial area, where the muri become radial. Proximal exine thin, trilete mark labrate, labra narrow.

DIMENSIONS.    30–40μm (Cramer & Diez, 1975); 29–44 μm (based on 75 specimens, present study), muri <1 μm wide and high.

REMARKS.    The spores may be double-layered and on some specimens a membranous curvatural zone is seen bearing radial extensions of the distal muri.

COMPARISON.    The tightly packed geniculate narrow distal muri distinguish this species. Cramer & Diez (1975) refer to a 'pronounced sculpture of brain-like muri' distally.

OCCURENCE.    Distributed through the **H** to lower **MN** Biozone (**NA** Sub-Biozone).

## *Chelinospora* cf. *hemiesferica* (Cramer & Diez) comb. nov.
Pl. 4, figs 6, 10; Pl. 9, fig. 4; Pl. 10, fig. 1

DESCRIPTION AND COMPARISON.    As for *C. hemiesferica,* but with broader, more widely spaced distal muri; muri more than 1–3 μm wide and 1–2 μm apart.

OCCURRENCE.    Found in all sections, Argovejo, Geras, La Peral and La Vid sections, Upper San Pedro Formation; range *hemiesferica*, **EC** Biozones to lower **MN** (**NA**) Sub-Biozone; found in the *hemiesferica* Biozone only in the La Peral Section.

## *Chelinospora lavidensis* sp. nov.                                     Pl. 9, fig. 2

1978c    *Iberoespora hemiesferica* Cramer & Diez; Rodriguez: 418, pl. 3, fig. 15.

1983    *Dictyotriletes geriense* Rodriguez: pl. 6, fig. 6 only.

DERIVATION OF NAME.    Named for the La Vid locality.

HOLOTYPE.    FM 1494 (Pl. 9, fig. 2), diameter 33 μm; sample Ger 9, slide D1/1, co-ord. 195 1056; E.F. no. U/36, upper San Pedro Formation, Geras section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS.    A *Chelinospora* with narrow low muri, 1 μm or less wide and >1μm high, forming an irregular reticulum with broad lumina.

DESCRIPTION.    Proximally hilate miospores, equatorially 2–4 μm thick, distal exine thick (not measured), amb subcircular to subtriangular. Proximal hilum thin, frequently broken or absent, trilete mark not seen. Equatorially and distally sculptured with an irregular reticulum, muri 1 μm or less wide, <1 μm high, lumina highly variable in shape and size on a single spore, at the distal pole large and polygonal 8–10 μm wide, subequatorially *c.* 1–2 μm wide; muri become radial at the equator. Y-mark with narrow 'folds' extends *c.* 2/3 spore radius and merge into crassitude at the hilum margin, frequently gape over much of the hilum forming a distinct triangular area.

DIMENSIONS.    29–43 μm (based on 17 specimens).

COMPARISON.    *Chelinospora hemiesferica* (Cramer & Diez) comb. nov. has a distal sculpture of closely packed geniculate muri but resembles *C. lavidensis* sp. nov. because both species have an equatorial band of radial muri.

REMARKS.    Several species of *Chelinospora* (*C. hemiesferica, C. sanpetrensis, C. media* and *C. lavidensis*) have a subequatorial band of muri normal to the equator, which may indicate affinity or possibly represents a feature related to the development of the tetrad in murornate spores.

OCCURRENCE.    Upper part of **H** and **EC** Biozones, rare in lower **MN** (**NA**) Sub-Biozone, Upper Přídolí and lowermost Devonian, Argovejo, Geras and La Vid sections.

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**PLATE 12**

Figs 1, 2    *Pseudoclathrochitina carmenchui* (Cramer 1964). **1,** FC 104, lateral view, × 350, Arg11A/508/12, (Q27/4); **2,** FC 105, LP20/SB5/54; **2a,** lateral view × 400; **2b,** basal margin detail, × 1100.

Fig. 3    *Margachitina elegans* var. *corta* (Cramer 1964). FC 106, lateral view, × 300, Arg12/510/8, (K30/4).

Fig. 4    *Urnochitina urna,* Eisenack 1934. FC 107, chain of 3 individuals, lateral view, × 220, LV10/492/9, (N34).

Fig. 5    *Margachitina elegans* Taugourdeau & de Jekhowski 1960. FC 108, lateral view, × 300, LV12/494/8, (N25).

Fig. 6    *Sphaerochitina sphaerocephala* (Eisenack 1932). FC 109, lateral view, × 700, Arg5A/SB7/4.

Fig. 7    *Fungochitina kosovensis* Paris & Kríz 1984. FC 110, LP19/SB5/57; **7a,** lateral view, × 200; **7b,** basal margin detail, × 1250.

Fig. 8    *Angochitina tsegelnjucki* Paris & Grahn 1996. FC 111, lateral view, × 200, Ger14/468/8, (P31/4).

Fig. 9    *Cingulochitina serrata* (Taugourdeau & Jekhowski 1960). FC 112, LV12/494/8, (N24), **9a,** chain of 11 individuals, lateral view, × 130; **9b,** detail of connection, × 500.

Fig. 10    *Angochitina echinata* Eisenack 1931. FC 113, LP8/CSB1/1; **10a,** lateral view, × 350; **10b,** neck detail, × 750.

Fig. 11    *Angochitina thadeui* Paris 1981. FC 115, LV5a/CSB1/8; **11a,** lateral view, × 200; **11b,** apertural detail, × 650.

Fig. 12    *Angochitina ambrosi ambrosi* Schweineberg 1987. FC 116, Ger8/461/8, (N38/3); **12a,** lateral view, × 200; **12b,** apertural detail, × 750.

Fig. 13    *Angochitina chlupaci* Paris, Laufeld & Chlupac 1981. FC 117, lateral view, × 250, Arg13/455/2, (J28/2).

Fig. 14    *Angochitina echinata* Eisenack 1931. FC 114, Ger9/456/7, (K31/1); **14a,** lateral view, × 300; **14b,** spiny ornament detail, × 850.
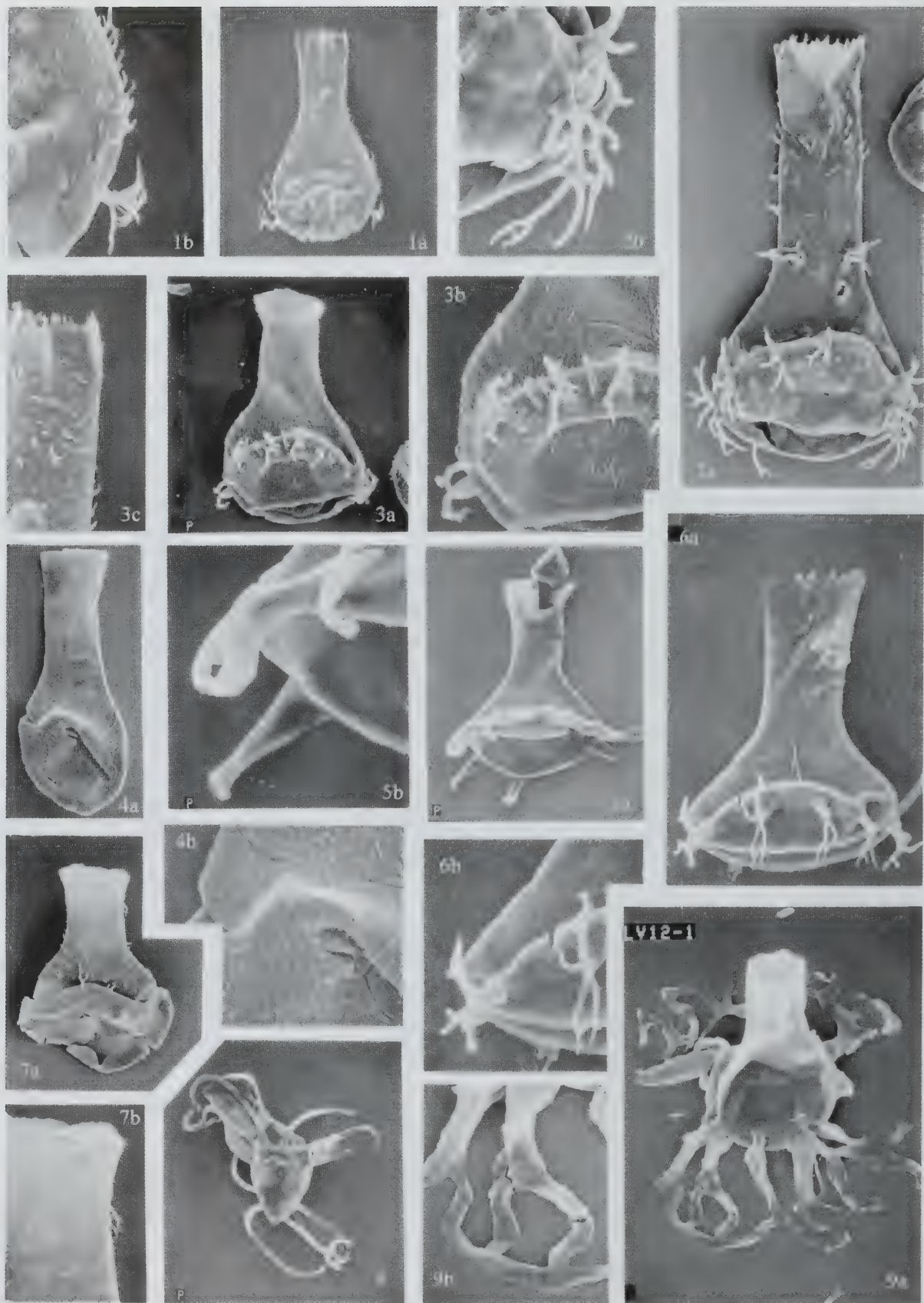
*Chelinospora media* sp. nov. Pl. 9, fig. 6

1978a *Chelinospora mariae* Rodríguez (pars): 10, pl. 1, fig. 4.

DERIVATION OF NAME. Latin *medius* a., intermediate.

HOLOTYPE. FM 1495, sample Argovejo 92/12 (510) 3, 093 1019, E.F. no. K32/2 J32/4; Lower San Pedro Formation, Argovejo section, Province of León, Cantabrian Mountains, northwest Spain.

DIAGNOSIS. A *Chelinospora* with low muri, <1 μm wide and < 1μm high, forming a regular reticulum with broad lumina of more or less even size.

DESCRIPTION. Proximally hilate miospores, equatorially 2–4 μm thick, distal exine thick (not measured); amb subtriangular. Proximal hilum thin, frequently broken, or absent, trilete mark not usually seen. Exine equatorially *c.* 5 μm, distally thick equatorially, but not measured. Equatorially and distally sculptured with a reticulum, muri 1 μm or less wide, 1–2 μm high, lumina relatively large, polygonal and 6–14 μm wide; muri become radial at the equator. A few specimens show a Y-mark, with sutures to the inner margin of the patina.

DIMENSIONS. 31–60 μm (based on 12 specimens); England, 37–67 μm (based on 37 specimens).

COMPARISON. Differs from *Chelinospora lavidensis* by the more regular reticulum with broad, more or less even, lumina. The holotype of *Chelinospora mariae* Rodriguez (1978a: pl. 1, fig. 3) appears to be conspecific with *C. cassicula* Richardson & Lister 1969, but other specimens figured by Rodriguez (1978a: pl. 1, fig. 4) appear identical to *C. media* sp. nov.

REMARKS. There appears to be a morphological gradation between *Chelinospora lavidensis*, *C. media*, and *C. cassicula* with some overlap in the ranges of the species. *C. lavidensis* occurs in the uppermost Přídolí and Lower Devonian (upper **H**, **EC** Biozones and lower **MN** Sub-Biozone) of the Cantabrian Mountains. *C. media* occurs near the Silurian/Devonian Boundary and in the lower **MN** Sub-Biozone, and is rare in the middle **MN** Sub-Biozone; *C. cassicula* occurs both in Spain and England in the lower **MN** Sub-Biozone, and especially the middle **MN** Sub-Biozone in England.

Two tryads/dyads (Richardson, 1996a: pl. 3, figs 1, 2) show such close similarities in sculpture to *C. media* that they probably were derived from the same, or closely similar, plants. All these *Chelinospora* species represent part of an evolving spore morphon and were probably derived from a group of closely related plants. The dyads of the species *Chelinohilates erraticus* Richardson 1996b: pl. 7, figs 5–7, have identical sculptural patterns.

OCCURRENCE. Upper San Pedro Formation, La Vid **EC** Biozone, Argovejo and Geras sections, lower **MN** Biozone, uppermost Silurian and Lower Lochkovian. Occurs in the lower part of the lower **MN** (**NA**) Sub-Biozone, Shropshire and Herefordshire in England.

*Chelinospora (Lophozonotriletes?) poecilomorpha*
(Richardson & Ioannides) comb. nov. Pl. 10, figs 6, 7

BASIONYM. *Lophozonotriletes? poecilomorpha* Richardson & Ioannides, 1973: pl. 7, figs 9–15; pl. 8, figs, 1, 4–6.

HOLOTYPE. Richardson & Ioannides, 1973: pl. 7, fig. 10, BP10/22-831060, C1-34 borehole, Libya.

REMARKS. This taxon is transferred to the genus *Chelinospora* because specimens studied under SEM and light microscopy show a distinct distal pattern with a thin polar proximal membrane.

*Chelinospora sanpetrensis* (Rodriguez) comb. nov.
Pl. 4, fig. 8; Pl. 7, fig. 10

BASIONYM. *Brochotriletes sanpetrense* Rodriguez, 1978c: 414, pl. 1, fig. 13.

1983 *Brochotriletes sanpetrensis* Rodriguez: 34, pls 1, 10, 19.

HOLOTYPE AND LOCUS TYPICUS. Rodriguez, 1978c: pl. 1, fig. 13; Torrestio, Province of León Cantabrian Mountains, northwest Spain, lower part of San Pedro Formation.

EMENDED DIAGNOSIS. A *Chelinospora* with a densely murornate, foveolate, and irregular foveo-reticulate sculpture with broad, sinuous, low muri, and narrow lumina.

DESCRIPTION. As in Rodriguez, 1978c: 414, but forms with a reticulum of wide muri and large rounded, polygonal and irregular lumina are classified as a separate species (*C. cantabrica* sp. nov.).

DIMENSIONS. 24, 29–49 μm (based on 60 specimens); 30–45 μm. (Rodriguez, 1978c).

REMARKS. The structure is patinate and consists of a thick distal exine and a thin proximal hilum, frequently ruptured, with a narrow fold on the inner margin of the curvaturae. Under the SEM some specimens show a sculpture of microrugulae and micrograna in the curvaturate zone. Specimens with a dominantly foveolate sculpture are referred to as *Chelinospora* cf. *sanpetrensis* but probably grade into the reticulate forms.

OCCURRENCE. Argovejo, Geras, La Peral and La Vid sections, lower and middle San Pedro Formation; range **RS** and lower to middle **H** Biozones; isolated specimens found in lower **EC** Sub-Biozone (Geras) and lower **MN** (**NA**) Sub-Biozone (La Vid).

Genus *CYMBOSPORITES* Allen 1965

TYPE SPECIES. *Cymbosporites cyathus* Allen 1965.

*Cymbosporites* cf. *dittonensis* Richardson & Lister 1969
Pl. 9, fig. 7

DIMENSIONS. 22–35 μm (based on 6 specimens).

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PLATE 13

Figs 1, 3c  *Palenchitina pisuergensis* Schweineberg 1987. FC 118, Ger7/SB7/6; **1a,** lateral view, × 300; **1b,** ornament detail, × 1000; **3c,** enlargement of part of Fig. 1a, × 1000.

Fig. 2  *Ancyrochitina valladolitana* Schweineberg 1987. FC 119, Ger4/CSB3/5; **2a,** lateral view, × 355; **2b,** appendix detail, × 750.

Fig. 3  *Ancyrochitina javieri* Schweineberg 1987. FC 120, Ger7/SB7/6; **3a,** lateral view, × 300; **3b,** basal margin detail, × 650.

Fig. 4  *Angochitina elongata* Eisenack 1931. FC 121, Ger9/456/7, (M32/1); **4a,** lateral view, × 300; **4b,** ornament detail, × 850.

Fig. 5  *Ancyrochitina fragilis brevis* Taugourdeau & Jekhowski 1960. FC 122, LV10/492/9, (L36/4); **5a,** lateral view, × 300; **5b,** appendix detail, × 1000.

Fig. 6  *Ancyrochitina libyensis* Jaglin 1986. FC 123, Arg4/SB7/3; **6a,** lateral view, × 500; **6b,** appendix detail, × 850.

Fig. 7  *Ramochitina villosa* (Laufeld 1974). FC 124, Ger2B/CSB3/3; **7a,** lateral view, × 400; **7b,** apertural detail, × 500.

Fig. 8  *Plectochitina rosendae* Cramer & Diez 1978. FC 125, lateral view, × 400, LV10/492/9, (H35/1).

Fig. 9  *Plectochitina carminae* Cramer 1964. FC 126, LV12/494/7, (P22/4); **9a,** lateral view, × 300; **9b,** appendix detail, × 600.

REMARKS. The Cantabrian material has close-packed wide based coni to spinose elements, some biform. The elements are not mixed with minute cone as in typical forms of the species.

OCCURRENCE. Rare, Upper San Pedro Formation, Argovejo, Lower **MN (NA)** Sub-Biozone.

### *Cymbosporites* sp. B                                                    Pl. 10, fig. 3

DESCRIPTION. Amb subtriangular to subcircular, usually preserved in polar compression. Proximal surface laevigate, contact areas covered by a thin diaphanous exine (hilum), near the periphery of the contact areas are distinct arcuate folds, which form a constant character, usually destroyed except near the margin. Outside the contact areas the exine is much thicker, equatorially and distally, 1.5–2 µm (measured equatorially). Sculpture confined to the equatorial margin and distal hemisphere; consists of broad based coni rounded in plan and evenly tapered in profile, *c.* 1.5 µm wide and >1 µm high; sculptural elements spaced, but with insufficient distance between them for elements of a similar size. Triradiate mark not seen apart from curvatural invaginations at the radial apices.

DIMENSIONS. 26–31 µm (based on 11 specimens).

COMPARISONS. Similar to *Cymbosporites* cf. *catillus* Allen 1965 in Richardson & Lister 1969 except that the coni are broad-based and larger.

REMARKS. Other specimens which may belong to the genus have been found in the Argovejo and Geras sections, namely ?*Cymbosporites* sp. A (Pl. 10, fig. 2) and *Cymbosporites* sp. (Pl. 10, figs 4, 5).

OCCURRENCE. Upper San Pedro Formation, Argovejo, Geras, and La Vid, **EC** Biozone and rare lower **MN (NA)** Sub-Biozone.

## TAXONOMY OF CHITINOZOA

As the main purpose of this paper is to define a spore biozonation for the Cantabrian region, only *Ramochitina villosa* (formerly *Gotlandochitina* Laufeld 1974) is described briefly here. A more detailed investigation of the chitinozoans from the Cantabrian Area is to be presented in a forthcoming publication. All material is deposited in the collections of the Natural History Museum, London.

Order **PROSOMATIFERA** Eisenack 1972
Family **LAGENOCHITINIDAE** Eisenack 1931, emend Paris 1981
Subfamily **ANGOCHITININAE** Paris 1981
Genus *RAMOCHITINA* Sommer & van Boekel 1964, emend.
Paris *et al.* 1999

TYPE SPECIES. *Ramochitina ramosi* Sommer & van Boekel, 1964: 426, pl. 1, fig. 3.

### *Ramochitina villosa* (Laufeld 1974)                            Pl. 13, fig. 7

1974    *Gotlandochitina villosa* Laufeld: 95, figs 7a, b.
1994    *Gotlandochitina villosa* Laufeld; Sutherland: 65, pl. 17, figs 7–14.

HOLOTYPE. LO 4587 T, figured Laufeld, 1974: fig 56a.

DIAGNOSIS. (After Laufeld, 1974: 95). Body spheroidal, neck cylindrical to subcylindrical; broadly rounded flexure. Ornament of spines which may exhibit simple branching; spines on apertural

portion of vesicle curved in aboral direction and in opposite direction on the apertural portion of vesicle; spines on neck decrease in size towards oral pole.

DISCUSSION. In the generic revision of Paris, Winchester-Seeto, & Grahn (2000) *Gotlandochitina* Laufeld 1974 is considered a junior synonym of *Ramochitina* Sommer & van Boekel 1964. *G. villosa* is here transferred to *Ramochitina*.

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